

# The American Midland Naturalist

Founded by J. A. Nieuwland, C.S.C.

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## Studies on the Collembolan Genus *Hypogastrura*

RIOZO YOSII

*Yoshida College, Kyoto University, Japan*

In earlier papers I have indicated the importance of chaetotaxy in the taxonomy of Collembola. Recently I have become particularly interested in the genus *Hypogastrura*, one of the most archaic genera of the order. The genus as so far known includes about a hundred cosmopolitan species. The species treated in this paper are not numerous and the specimens available for study few in number, yet it is quite possible that the general trends in the chaetotaxy of the group can be seen here, and the conclusions drawn from this material are probably applicable to most of the members of the genus.

A number of my colleagues of collembology furnished much of the material upon which this study was made. I wish to extend my sincere thanks to Dr. K. Christiansen (USA), Dr. D. L. Wray (USA), Dr. Marie Hammer (Denmark), and Dr. F. Carpentier (Belgium). The specimens described in this paper are in my personal collection. The study of the chaetotaxy of this group has already been outlined by Bonet (1945, 1947), Stach (1946), Gisin (1946, 1949), and Yosii (1956). In the last mentioned paper I described the basic chaetotaxy in the Family Hypogastruridae and named each seta of the head and body segments. This nomenclature is followed in the present paper, although it should be noted that the form that I originally described as typical of *Hypogastrura* is actually that found in a member of *Ceratophysella*, and thus some modifications must be made. For convenience, the setae are illustrated in the Key Figure together with abbreviations of technical terms used in the description of species.

The 20 species of *Hypogastrura* here treated and described, and those whose chaetotaxy is already known, may be split into three subgenera as follows:

1. S.s. upon Th. II, III is  $p_4$  ..... 2  
S.s. upon Th. II, III is  $p_3$  Ant. III/IV with or without eversible antennal  
sac ..... *Ceratophysella*
2. Accessory tubercle of P.A.O. is enclosed by two posterior tubercles of that  
organ. Eversible antennal sac usually present ..... *Cyclograna*  
Accessory tubercle of P.A.O. is located apart from it. Eversible antennal  
sac absent ..... *Hypogastrura*

Subgenus *Ceratophysella* Börner, 1932Type: *Hypogastrura* (*C.*) *armata* Nicolet

The subgenus may be divided into groups in the following manner:

1. Upon Abd. IV,  $p_1$  longer than  $p_2$ .  $M_1$  upon Abd. I-III absent ..... 2  
     Upon Abd. IV,  $p_1$  shorter than  $p_2$ . Small  $m_1$  upon Abd. I-III present .....  
     ..... *communis* Group
2. Upon Abd. IV both  $p_2$  and  $p_3$  short. S.s. is  $p_5$  ..... *armata* Group  
     Upon Abd. IV,  $p_2$  short and  $p_3$  long. S.s. is  $p_4$  ..... *denisana* Group

## THE COMMUNIS GROUP

This group has the chaetotaxy of Gisin's a-Type (1947) and is represented by the figure of *H. troglodites* Yosii and *H. communis exilis* Yosii 1956.

*Hypogastrura communis* (Folsom)

## Fig. 2

Folsom, 1897, Kinoshita, 1916; Denis, 1927, 1936.

Syn. nov. *Hypogastrura yuasai*: Yosii, 1954 Oyo-Kontyu 10: 137.

The species has been thoroughly studied by Denis 1924, 1925 with Japanese and Indian material. The species is clearly different from *H. armata* in the chaetotaxy of Abd. IV, where  $p_2$  is greater than  $p_1$  and  $p_3$ . This type of chaetotaxy is represented in Europe by *H. denticulata* Bagnall 1941 (see Gisin 1949). The species has some color variations.

*Hypogastrura communis* f. *principalis* (nov. forma)

Body color intensely blue black. This type is very common in central Japan and frequently emerges in huge numbers from decaying straw in rice fields in late autumn. It is also found in China and Kashmir. *H. yuasai* Yosii, 1954 from Japan is a synonym of the present form. Recently I examined some individuals of this species from Okinawa (M. Nagayama, collector).

*H. communis* f. *exilis* Yosii

Syn. *H. communis exilis*, Yosii 1956.

Body color brownish gray or dark brown. This color form is abundant in Japan all through the year and is often fungivorous or cavernicolous. What I have previously reported from Taiwan as *H. armata* Nic. is, in reality, the present form.

*Specimens seen*.—I have seen 10 specimens from North America (all from Banff, Alberta, Canada) referable to the present species (31 VII 1950, K. Christiansen). Another 20 specimens from Back Bone Mt., vicinity of Thomas, West Virginia (18 VI 1950, K. Christiansen) are also referable to the present form. The latter are rather young individuals and not to be determined with certainty.

The following species are to be included to the *communis* Group:

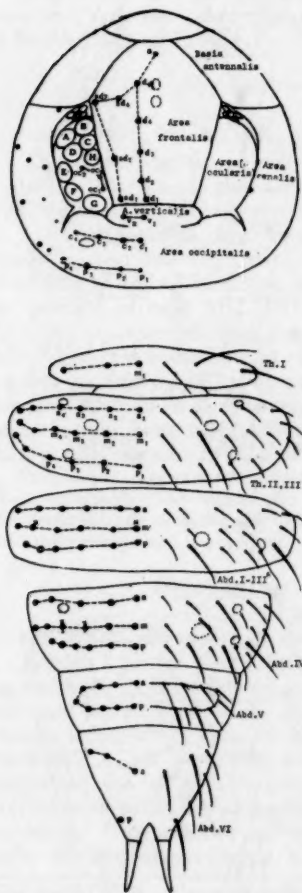
*H. troglodites* Yosii, 1956.—Antenna without eversible sac. Body color pale; Japanese caves.

*H. quinqueoculata* Yosii, 1956.—Eyes 5 per side. Dentes with 5 setae; Japanese caves.

*H. fukugakuchiana* Yosii, 1956.—Eyes 4 (or 3) per side. Dentes with 6 setae; Japanese caves.

*H. proserpinae* Yosii, 1956.—Eversible antennal sac rudimentary. Dentes with 6 setae. Mucro without outer lobe. Abd. IV with s.s. at the position of P<sub>4</sub>. (Fig. 3.)

*H. denticulata* Bagnall, 1941.—Unguis very slender; England, Switzerland.

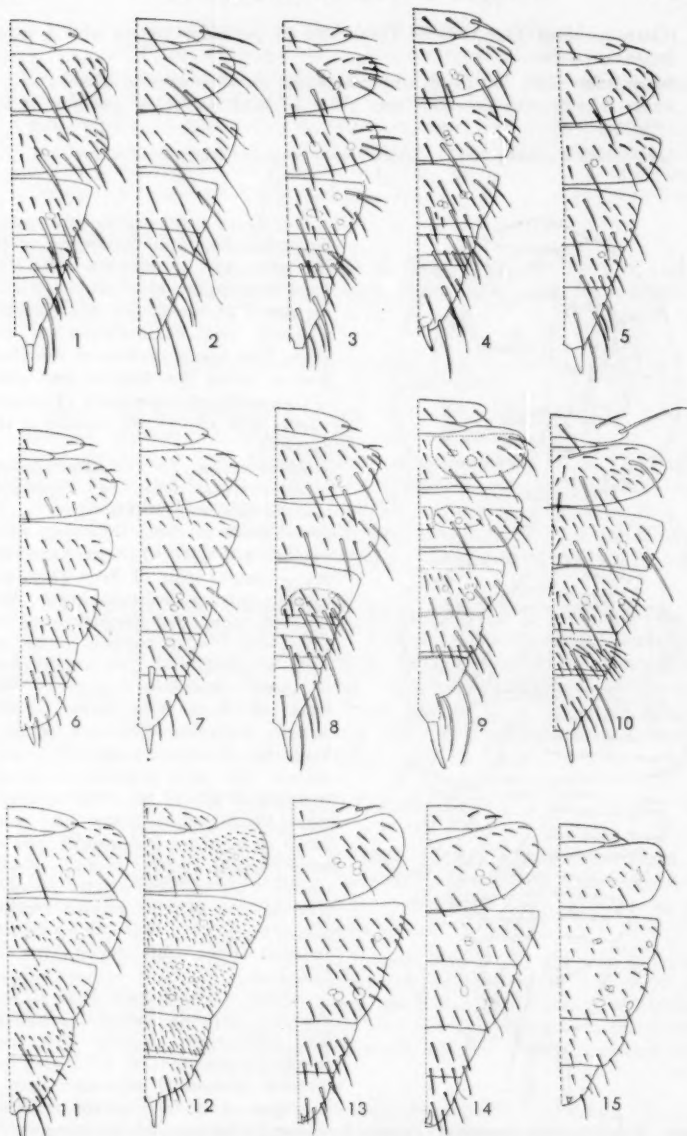


Key figure.—Illustration of a typical hypogastruran with abbreviations for the nomenclature of each seta. The right side of the head shows its subdivision into areas; the left, the distribution and nomenclature of the setae. The lower portion of the illustration shows the tergites and setae of *Geratophysella communis* (Folsom). (Setae with an "x" are missing in the example.)

**Abbreviations for the nomenclature of each setae.** HEAD: a—unpaired anterior seta on Area Frontalis; d<sub>1-5</sub>—dorsal setae of Area Frontalis; sd<sub>1-5</sub>—subdorsal setae of Area Frontalis; oc<sub>1-3</sub>—ocular setae of Area Frontalis; (suffix number indicates each seta counted from the proximal one as 1, 2, 3—); v<sub>1-2</sub>—vertical setae of Area Verticalis; p<sub>1-4</sub>—parietal setae of Area Occipitalis; c<sub>1-4</sub>—cervical setae of Area Occipitalis; (suffix number indicates each seta counted from the dorsal one as 1, 2, 3—). TRUNK: s.s.—seta sensalis, a specially modified seta of the tergite, usually more slender than others and with broad socket; a-row—anterior row of setae on each tergite; m-row—middle row of setae on each tergite; p-row—posterior row of setae on each tergite; (a<sub>1-6</sub>, m<sub>1-6</sub>, p<sub>1-6</sub> indicates each seta counted from the dorsal one as 1, 2, 3—).

**Other abbreviations:** Ant. I-IV—the 1st, 2nd-4th antennal segment; Th. I-III—fore, middle and hind thoracic segment; Abd. I-VI—the 1st, 2nd-6th abdominal segment; Ung<sub>1-3</sub>—Unguis of the fore, middle and hind

legs; P.A.O.—postantennal organ; fovea—rounded spot of the integument, where the skin granules are wanting; fovula—rounded spot of the integument, where the skin granules are minute; AH—anal horns; Man—manubrium; D—dentes and Mu—mucro.



Figs. 1-15.—1. *Hypogastrura (Ceratothysella) communis* (Folsom). 2. *H. (Ceratothysella) proserpinae* Yosii. 3. *H. (Ceratothysella) armata* Nicolet. 4. *H. (Ceratothysella) pseudarmata* (Folsom). 5. *H. (Ceratothysella) deni-*

Questionable species of the *communis* Group:

- H. engadinensis* Gisin, 1949.—Eversible antennal sac rudimentary or absent; Switzerland.  
*H. succinea* Gisin, 1949.—Dentes with 6 setae. Anal spines succinic in color; Switzerland, Germany, Jan Meyen Is.

THE ARMATA GROUP

The chaetotaxy of this group represents Gisin's b-type (1947). I have seen only two species belonging to the group, although they seem to be common in Europe.

*Hypogastrura armata* (Nicolet)

Fig. 3

Nicolet, 1841; Börner, 1932; Stach, 1949; Gisin, 1949.

The diagnostic structures of this species have already been described by Stach and other authors. Chaetotaxy of head normal. Ventral side of antennal segment IV has 10-15 small, peg-like setae. Th. II, III with setae in three rows (a-, m-, and p-). S.s. is at the position of  $p_3$  and is as large as  $p_2$ .  $M_2$  is rather long and often dislocated somewhat distally. Small pit before s.s. One additional s.s. lateral at the position of  $m_6$ . Abd. I-III with setae in two rows (a- and p-).  $P_5$  is s.s.;  $p_2$  is longer than the other setae of the row. No m-row dorsally. Abd. IV with setae in three rows.  $P_1$  is much larger than subsequent  $p_2$  and  $p_3$ .  $P_4$  is again large.  $P_5$  is s.s. and as long as  $p_4$  but slender. Abd. V with coarsely granulated area at about its middle. Setae in two rows, arising from the margin of this area.  $P_1$  larger than  $p_2$ .  $P_3$  appears to be a little modified. Abd. VI with s.s. as usual.

*Specimens seen*.—One example from Grunwald, München, Germany (R. Yosii, collector). This supposedly well-known species is known with certainty only from Europe. All records from other parts of the world must be tentative until their chaetotaxy is examined.

*Hypogastrura pseudarmata* (Folsom)

Figs. 4, 24-29

Syn. *Achorutes pseudarmata* Folsom, 1916.

Length 1.5 mm. Color dark brown or blackish brown. Ant. IV has an end-bulb slightly divided into two parts, accompanied by a socket hair and some weak setae. There are also slender and well-defined sensory setae, seven dorsally and about twenty small, peg-like setae ventrally. As all specimens were rather contracted, the eversion of antennal sac was not seen, but it may be present. The organ of Ant. III normal and with two accessory setae. P.A.O. in deep fold of the integument. Two anterior elements are much larger than the posterior ones. An accessory tubercle is very conspicuous. All of these organs

*sana* Yosii. 5. *H. (Ceratophysella) glancei* Hammer. 7. *H. (Ceratophysella) duplicispinosa* Yosii. 8. *H. (Cyclograna) vulgaris* n. sp. 9. *H. (Cyclograna) lorica* n. sp. 10. *H. (Cyclograna) horrida* n. sp. 11. *H. (Cyclograna) gibbomucronata* Hammer. 12. *H. (Cyclograna) pilosa* Yosii. 13. *H. (s. str.) nivicola* (Fitch). 14. *H. (s. str.) copiosa* (Folsom). 15. *H. (s. str.) christianseni* n. sp.

together are about as large as one eye in diameter. Tibiotarsus has one tenent hair, whose distal end is slightly knobbed, or blunt. Unguis elongate, distally acuminate and with one inner tooth and a pair of lateral teeth. Unguiculus setaceous, about two-thirds as long as the unguis and with a broad basal lamella. Ventral tube with four setae per side. The rami of the tenaculum with four teeth. Dentes of the furca coarsely granulated on dorsal side and with seven setae almost of equal length. Mucro granulated along its shaft and is typically of *armata* type. Anal spine smaller than that of *H. armata* and is about two-thirds as long as the mucro of the third unguis (inner side). Anal lobe well developed. The profile of Abd. VI quite different from that of *H. armata* (Folsom, 1917). Chaetotaxy typical of the type; but s.s. is so poorly developed upon Th. II, III, and Abd. I, as to be found only by the neighboring pit, which is very conspicuous. Abd. I-III with two rows of setae.  $P_5$  is s.s., small on Abd. I and normally long on Abd. II and III.  $M_1$  is absent. Abd. IV with three rows of setae.  $P_1$  is large, while  $p_2$  and  $p_3$  are small. Abd. V with a granulated middle area.

*Specimens seen*.—Fifteen specimens from Arlington, Massachusetts, USA. (15 XI 1950, K. Christiansen.)

I have two specimens of *H. sigillata* Uzel to which the species is closely allied. These specimens were collected in arctic Canada and sent by Dr. Marie Hammer. The specimens were already mounted and I could not observe all the setae of the body. Yet s.s. of Th. II is well developed. These two species must therefore be separated.

The following species are to be included in the *armata* group:

- H. gibbosa* Bagnall, 1940; Gisin, 1949.—A pair of setae of Area Ocularis and of Area Frontalis converted to spines; England, Switzerland.  
*H. granulata* Stach, 1949.—Abdominal segments with granulated areas; Poland, Ukraine, Slovakia.  
*H. luteospina* Stach, 1919.—Anal horns queerly modified; Poland, Ukraine.  
*H. cavicola* Börner, 1901; Stach, 1949.—Eversible antennal sac absent, body color reduced; caves of Hungary, Austria, and Germany.  
*Typhlogastrura balazuci* Delamare, 1951.—From a French cave; has chaetotaxy of the *armata* type.

#### THE DENISANA GROUP

This is apparently a branch of the *armata* Group. On Abd. II-III,  $m_1$  is always absent as in *H. armata*. An Abd. IV, however,  $p_1$  is large,  $p_2$  small, and  $p_3$  is absent. So, s.s. is the position of  $p_4$ , instead of  $p_5$  as in the *armata*-type. Generally,  $m_2$  on Th. II, III has a tendency to move posterior near to  $p_2$ .

#### *Hypogastrura denisana* Yosii Fig. 5

Yosii, 1954, 1956.

As figured in Yosii, 1956 (Plate IV, Fig. 38),  $m_2$  on Th. II, III and  $p_2$  on Abd. I-III are large. Abd. IV has the chaetotaxy as stated above. I have erroneously described the s.s. of this segment as  $p_5$

(*loc. cit.*, p. 17). It is actually  $p_4$ . On Abd. V, the setae of p-row are larger than a-row (erroneously figured in Fig. 38). The species is distributed all over Japan.

*Hypogastrura glancei* Hammer

Fig. 6

Hammer, 1953.

Type specimens sent to me by Mrs. Hammer reveal the chaetotaxy of *denisana*-type. Body setae relatively small. Th. II, III with  $m_2$  thicker than others, but not especially long and often moved near to  $P_2$ .  $P_3$  is s.s. and not long. Abd. I-III with  $p_2$  larger than others, and  $p_5$  s.s. Abd. IV with  $p_1$  largest,  $p_3$  second largest, and  $p_2$  small.

*Specimens seen.*—Two specimens from Coppermine, Arctic Canada (M. Hammer, collector).

*Hypogastrura duplicispinosa* Yosii

Fig. 7

Yosii, 1954, 1956.

As has been stated, the species has the *denisana*-type of chaetotaxy.  $P_1$  on Abd. V is converted to a spine; Japan.

I can find no reliable data to place other species in the *denisana* Group. Only *Schafferia duodecimocellata* Bonet, 1946 from a Mexican cave has the chaetotaxy of *denisana*-type.

Subgenus *Cyclograna*

The subgenus includes species characterized by the peculiar forms of the P.A.O. In the chaetotaxy, s.s. on Th. II, and III is  $p_4$  in contrast to  $p_3$  in the subgenus *Ceratophysella*. The eversible sac of the antenna is always present among known forms of *Cyclograna*. Some species of the group have setae of the head converted to spines (*H. franzi*, *pilosa*, *horrida*, etc.). The subgenus has the tendency towards increased body setae. The first step is seen in *H. horrida* and *H. gibbomucronata* in which, although the arrangement of setae is irregular, one may find larger setae distinctly different from others in each position. Such a condition, I should like to designate as "Plurichaetosis." This augmentation of setae continues until there is no longer any distinction between individual setae, and the body segments are covered uniformly with many small setae (*H. pilosa*). To such a state of chaetotaxy, I have proposed the name "Polychaetosis."<sup>1</sup> Such polychaetosis is not only found in *Cyclograna* but also in such genera of the arthropleon collembola as *Anurida*, *Homaloproctus*, and *Tetrodon-tophora*. Examples of plurichaetosis include almost all species of the genus *Onychiurus*, which has arisen apparently from *Tullbergia* in which the chaetotaxy is not at all complicated.

*Hypogastrura (Cyclograna) vulgaris* n. sp.

Figs. 8, 30-36

*H. armata*: Foisom, 1916.

Length 1.3 mm. Color bluish-gray. The pigment is aggregated

<sup>1</sup> R. Yosii, in 80th Jubilee Volume of Prof. Stach of Krakow (in Press).

into patches. Antennae dark. Legs, furca, and ventral side of the body pale. End-bulb of Ant. IV located in a groove and accompanied by many setae with basal sockets. There are seven elongated sensory hairs dorsally and about twenty-five small, but very conspicuous, peg-like setae ventrally. Ant. III/IV with eversible sac. Third antennal organ is of two small rods in a shallow groove accompanied by two slightly modified setae. Eyes eight per side upon black eye-patches. P.A.O. is Gisin's h-type, i.e., the anterior two elements are situated almost in a straight line, while the posterior two have between them an elliptical accessory tubercle. Unguis elongate and with one internal tooth and a pair of lateral teeth. Unguiculus setaceous, reaching to about one-half of the unguis and with a rounded basal lamella. Tenent hair is not especially differentiated and not swollen at apex. Ventral tube with three (?) setae on each side. Rami of the tenaculum with four teeth. Mucro typically of *armata*-type; with broad outer lobe and basally granulated. Dentes dorsally granulated and provided with seven setae of which four on the inner side are remarkably thickened. Dentes to mucro as 2/1. Mu/Ung<sub>3</sub> as 2/3. Anal spines well-developed, very long with basal papillae touching at their bases. Anal spine (papillae included) to Ung<sub>3</sub> as 17/9. Chaetotaxy of head normal. Base of antennae well separated from frontal area by smaller granulation of the integument. The setae of the latter normal, d<sub>2</sub> stronger than others and positioned more lateral than usual. Segmental margins of the trunk with finer granulations than the middle portion and their boundaries of the finely granulated areas well defined. Th. I with 3 + 3 setae in a row. Th. II, III with three rows of setae. P<sub>2</sub> is long. M<sub>2</sub> is short. S.s. is p<sub>4</sub>. Abd. I-III with two rows and with a small m<sub>1</sub> as in *H. communis*. A<sub>2</sub> lies more lateral in position than usual. Abd. IV is distinctly tuberculated laterally and all setae except a<sub>1</sub> are located here. The arrangement of these setae is of the *communis*-type. Abd. V with two rows of setae. The segment is coarsely granulated at the middle portion. P<sub>1</sub> is extremely large and often dislocated anteriorly.

*Holotype*.—One male from Corvallis, Oregon, USA. (21 XII 1949, V. Roth, collector).

*Paratypes*.—Twelve specimens from the same locality and ten from Cambridge, Massachusetts, USA (25 IX 1949, K. Christiansen, collector).

Judging from Folsom's figures (1916, Proc. U.S. Nat. Mus. 50: 491) this species may be the same as his *H. armata*. Whether the present name becomes synonymous with Packard's *A. boletivorus*, *texensis*, *marmoratus* or *pratorem* must be determined after examining his type specimens.

#### *Hypogastrura (Cyclograna) loricata* n. sp.

Figs. 9, 37-40

Body length 1.7 mm. Color dark brown or brownish gray. Antennae well-pigmented. Segmental margins, ventral side of body, and

extremities paler. Ant./Head as 7:10. Ant. IV with an end-bulb deeply inserted in a groove accompanied by some socketed setae. Dorsally, there are seven sensory hairs of relatively small size. Peg-like setae of the ventral side are small but numerous. Ant. III/IV with an eversible sac. Only two accessory hairs of the third antennal sense organ can be seen. A sensory groove with two rods is apparently present, each masked by the rough granulation of the skin. Ant. II and I each with only one row of setae. Each antennal segment is very coarsely granulated and sharply contrasted with their minutely granulated borders. The antennal bases and the cervical margin are minutely granulated, in contrast with the frontal area. Eyes eight on a side, upon black patches. P.A.O. of *vulgaris*-type. Setae of frontal area very long and 3 + 3 in number;  $sd_1$ ,  $sd_4$  and  $sd_5$  are converted into spines. Area verticalis separated from other parts by a furrow and  $v_2$  is much longer than  $v_1$ . Unguis normal with one internal tooth and one lateral tooth. Unguiculus setaceous, with two rounded, broad lamellae. Tenent hair absent. Ventral tube with 4 + 4 setae. Rami of the tenaculum with four tenent. Dentes of the furca dorsally granulated with seven setae; the three setae of the inner row are thick. Mucro distally rounded with a broad, hyaline outer lobe. Each segment of the body with a remarkable granulated portion at about the middle zone. Upon Th. II, III and Abd. I-III, these granulated portions are divided medially by finely granulated areas along the dorsal midline and where  $a_1$ ,  $m_1$ , and  $p_1$  or  $a_1$  and  $p_1$  are located. Other setae are all on the granulated area. Upon Th. II and III,  $p_2$  and  $p_5$  are long. S.s. is  $p_4$ , which is small and often dislocated proximally. On Abd. I-III the coarsely granulated area is relatively small.  $M_1$  is distinctly present.  $P_2$  and  $p_4$  are long. S.s. is long and in position of  $p_5$ . Abd. IV with three rows of setae. The segment is coarsely granulated on the anterior two-thirds of the segment, and it is not divided medially.  $P_1$  and  $p_2$  almost equally long.  $P_3$  is small.  $P_4$  is s.s. (?). Abd. V coarsely granulated over most of the segment except its margin. This condition is in contrast to the granulation of Abd. V in other species such as *armata*, *communis*, and *vulgaris*, where only the portion between two rows of setae is coarsely granulated.

On Abd. VI, the granulations are extremely coarse upon the papillae. These, in turn, are so large that the segment is constricted on their bases, where  $a_1$  is inserted. Anal horns (AH) very long, yellow in color and gradually tapering to the end. AH/Mu as 2:1. AH/Ung.<sub>3</sub> as 4:3.

*Holotype*.—One male from Mount Washington, New Hampshire, USA (30 VIII 1949, K. Christiansen, collector).

*Paratype*.—Eight specimens from the same lot.

The species exhibit no plurichaetosis and may be distinguished from other species by three cephalic horns per side and the peculiar granulation of the integument.

*Hypogastrura (Cyclograna) horrida* n. sp.

Figs. 10, 41-45

Body length 1.6 mm. Color chestnut brown. Dorsal side of the body mottled with dark spots. Ant/Head as 17:15. Ant. IV with an end bulb concealed in a groove, accompanied by a conspicuous socket-seta. Sensory hairs of dorsal side more than 5, slender and well-developed. Ventral side thickly beset with numerous peg-like setae, more than fifty in number. Ant. III/IV with eversible sac. Third antennal organ and companion setae normal. Area Antennalis of the head clearly distinguishable from Area Frontalis which carries elongated, filiform setae and two cephalic spines per side which represent  $sd_4$  and  $d_5$ . P.A.O. typical for *Cyclograna*. Eyes eight per side, upon black patches. Area Verticalis is distinctly separated. Th. I with 3 + 3 setae in a row. All segments beyond Th. II are very unusual in their chaetotaxy. Although the distinction between large and small setae is still preserved, the small setae are numerous and irregular in position (plurichaetosis). On Th. II, III, one may find along its posterior margin  $p_2$ ,  $p_4$  (s.s.), and large  $a_2$  and  $m_5$  (?). On Abd. I-III,  $p_2$ ,  $p_4$  and  $p_5$  (s.s.) are large. Upon the segments beyond Abd. IV, s.s. is no longer seen. The integument is regularly granulated and each segmental margin has finer granulation. The larger granules increase in size posteriorly on Abd. IV-VI, and Abd. V is distinguished by two coarsely granulated zones at about the middle of the segment. Anal horns elongate, yellowish brown in color, and located upon conspicuous papillae which are somewhat separate. The longest setae of the body are not feathered. Unguis normal. Unguiculus setaceous, half as long as the unguis, and with rounded basal lamella. Tenent hairs not apparent. Ventral tube with four setae per side. Dentes of furca dorsally granulated and with seven setae (5 thick and 2 normal). Mucro with well-developed outer lobe and rounded apex.

*Holotype*.—One female from Corvallis, Oregon, USA (26 XII 1950, V. Roth, collector).

I have seen some individuals from the Japanese alpine region which are very near to the present form. As they are apparently immature, I am awaiting new material before determining them.

*Hypogastrura (Cyclograna) gibbomucronata* Hammer

Fig. 11

Hammer, 1953.

A type-specimen sent by Hammer is plurichaetotic. Setae upon head normal in position. Area Frontalis somewhat coarsely granulated.  $D_2$  and  $sd_4$  larger than others. Th. I: 3 + 3 setae. Th. II, III: setae of the posterior row fairly normal in position.  $p_4$  is s.s. and not large. The other rows are plurichaetotic except along the median dorsal line. The plurichaetosis is more prominent upon Th. III than on Th. II. Abd. I-III with p-row showing a clear distinction between large and small setae. S.s. is situated just posterior to a fovea. Abd. IV with p-row normal in location.  $p_5$  is s.s. Abd. V with a coarsely granulated area at about the middle of the segment. Setae approxi-

mately in two rows and  $p_3$  is s.s. Abd. VI is polychaetotic laterally.  $A_1$  is relatively small and is placed just before the anal papillae.  $A_2$  is large.

*Specimens seen*.—One specimen from Reindeer Station, Arctic Canada (M. Hammer, collector).

*Hypogastrura (Cyclograna) pilosa* Yosii  
Fig. 12

Yosii, 1956.

The chaetotaxy of this interesting species showing typical polychaetosis has already been described. In the present report, I will add only the figure showing all body segments. The species is known only from middle and southern Japan.

As the subgenus *Cyclograna* is characterized by its peculiar P.A.O., the species belonging to it are easily recognized from the literature. They are:

*H. franzi* Butschek et Gisin, 1949.— $D_2$  and  $sd_4$  of the frontal area converted to spines; Austria.

*H. hystrix* Handschin, 1924, Gisin, 1949.—Dens with 5 setae, body hairs strongly barbate; Switzerland, Austria.

*H. californica* Bacon, 1914.—One long spine on each segment; USA.

We have in addition to these two species with multituberculate P.A.O. and mucro similar to that of *H. armata*.

*Mitchellania hermosa* Wray, 1953.—Head with two spines per side; USA.

*H. monstrosa* Gisin, 1949.—Setae of Abd. IV of *communis*-type; Switzerland.

Subgenus *Hypogastrura* Bourlet, 1939 (*sensu* Gisin, 1955)

Type: *Hypogastrura (H.) viatica* (Tullberg)

The subgenus is characterized by the position of s.s. on Th. II and III, and by the lack of an eversible sac on the antenna; as well as by the relatively small and simple form of the P.A.O. Body setae usually short and the difference between long and short setae not conspicuous. We may divide the subgenus into the following groups by their chaetotaxy:

1. Area Verticalis confluent with Area Occipitalis and provided with only 1+1 setae ..... *nivicola* Group
- Area Verticalis is confluent with Area Occipitalis, or not, and always provided with 2+2 setae ..... 2
2. Abd. V with three transverse rows of setae ..... *christianseni* Group
- Abd. V with two rows of setae ..... 3
3. S.s. upon Abd. I-III; Abd. IV and Abd. V is  $p_4, p_4, p_2$  in position ..... *reticulata* Group
- S.s. upon Abd. I-III; IV and Abd. V is  $p_5, p_5$  and  $p_3$  in position ..... 4
4. Tenent hair 1, 1, 1 ..... *manubrialis* Group
- Tenent hair usually 2, 3, 3 ..... *viatica* Group

The latter two groups are only provisional and their members must be re-examined.

## THE NIVIGOLA GROUP

This group is characterized by its having only 1 + 1 setae on the Area Verticalis, which is fused with the Area Occipitalis. Tenent hair 1,1,1 and sensory hairs of Ant. IV usually rod-like. Only the three species here described are known, although there must be more species to be included in this group.

*Hypogastrura (s. str.) nivicola* (Fitch)

Figs. 13, 46

Syn. *H. socialis*: Uzel, 1890; Stach, 1949.

The American examples of the species agree with the description of Stach, 1949. P.A.O. with one large accessory tubercle. Dens with seven setae dorsally, normal in position. The inner side of the basal half of the mucro slightly lobed (cf. Stach, 1949, p. 76 and Plate IV, Figs. 6-9; not shown in Folsom's 1902 or 1916 figures). Distal end of the dens with a cap-like thickening of the integument on its ventral side (cf. Stach, 1949, Plate IV, Figs. 7, 9). Most body setae equally long and simple except on Abd. IV, V, and VI, where some of the larger setae are slightly feathered. Area Verticalis of head not divided from Area Occipitalis and with only 1 + 1 setae. Th. II-III with  $m_2$  apparently missing;  $p_4$  is s.s. Abd. I-III with most setae of equal length and  $p_5$  is s.s. Abd. IV with setae in three rows; but as  $m_1$  is missing, dorsal group apparently in two rows;  $p_5$  is s.s.  $p_1$  and  $p_4$  slightly longer than others. Abd. V with  $p_3$  s.s.;  $p_{3s}$  and  $p_5$  longer than  $p_2$ . Abd. VI with all setae long.

*Specimens seen*.—Four specimens from Peterborough, New Hampshire, USA (14 V 1950, K. Christiansen, collector). Fifteen specimens from Richland (?), Pennsylvania, USA (1 VI 1940, S. W. Frost, collector).

*Hypogastrura (s. str.) copiosa* (Folsom)

Figs. 14, 48-53

Folsom, 1916.

Syn: *Achorutes schneideri* Guthrie, 1903 (*nec* Schaffer).

Body length about 1.5 mm. Color brownish black except for ventral side and extremities. Ant. IV with an end-bulb in a deep groove. Sensory setae of the dorsal side short, blunt and rod-like in appearance, about 9 in number. Eyes eight per side, upon black patch. P.A.O. composed of four minute elements in a shallow groove, directly before eyes and about 1/2 to 1/3 of an eye in diameter. Accessory tubercle not mentioned. Third antennal segment organ of two rods without groove and with two guard setae nearby. Ungues of all legs equal, with an inner tooth near apex. Lateral tooth not to be seen. Unguiculus setaceous, half the length of the unguis and with a narrow, rounded basal lamella. Tenent hairs 1, 1, 1, very long and thick, distally not narrowed, and truncate. Ventral tube with four setae per side. Rami of the tenaculum 4-toothed. Dorsal side of dens smooth, with seven long setae. Mucro small, almost straight and only slightly rounded apically. D/Mu as 22:5. Mu/Ung<sub>3</sub> as 5:12. One unclear

outer lobe often seen. Anal spines small, acute, on basally contiguous papillae which are as long as the spines. An.sp./Mu as 7:5. All body setae moderately developed, somewhat stout and blunt (as in *H. viatica*); longer ones slightly serrate; s.s. setaceous. Area Verticalis confluent with Area Occipitalis and with only 1+1 seta as in *H. nivicola*. Th. II, III with setae in three rows.  $P_4$  is s.s. and slightly longer than others. Abd. I-III with setae in three rows.  $P_5$  is s.s. All setae equally long. Abd. IV with setae in three rows and  $p_5$  s.s. Abd. V with setae in two rows,  $p_3$  s.s. and longer than others.

*Specimens seen*.—Eight specimens from Cochetopa Pass, Colorado, USA (9 VII 1950, K. Christiansen, collector).

*Hypogastrura* sp. (?)

Syn: *Neogastrura reticulata* Hammer, 1953 (nec Börner).

Specimens from the Canadian arctic determined by M. Hammer as *H. reticulata* do not belong to this species. They differ from Japanese specimens identified as *H. reticulata* Börner in not having a well-developed tenent hair on each tibiotarsus. I have received two specimens already mounted in Salmon's fluid from Miss Hammer. As they are in a lateral position and intensely pigmented, I am unable to determine their chaetotaxy. Only the head capsule is available for this purpose, and here I can find the Area Verticalis is fused with the Area Occipitalis and provided with 1+1 setae. In view of this, this species—which I am unable to identify—must be included in the *nivicola* Group.

THE CHRISTIANSENI GROUP

The present group is easily identified by having three rows of body setae upon Abd. V. The group is represented by only two species at present.

*H. christianseni* n. sp.—All body setae simple; USA.

*H. itaya* Kinoshita.—Some of the setae on Abd. V and VI are long and distinctly swollen terminally; Japan.

*Hypogastrura christianseni* n. sp.

Figs. 15, 54-61

Body length 1.5 mm. Color blackish gray. The pigment is in blotches especially dense on the posterior part of the head. Antennae well-pigmented. Ventral side pale. Extremities almost unpigmented. Ant./Head as 1:1. Ratio of antennal segments I-IV as 10:12:13:17. Ant. IV with a terminal bulb in a deep pit accompanied by 2-3 weak setae and 7 well-developed, curving sensory setae. No eversible sac on Ant. III/IV. Third antennal segment organ composed of two small rods in a shallow groove and two modified companion setae. P.A.O. about 1.5 times the diameter of an eye and composed of four subequal elements. Accessory tubercle not found. Leg with one prominent tenent hair ending in a small bulb. Unguis well-developed and with one inner tooth. Unguiculus spiniform and equipped with a very narrow basal lamella, which is not larger than the basal papilla of the ungui-

culus. Ventral tube with 4+4 rather long setae. Rami of the tenaculum with three teeth. Furcula well-developed. D/Mu as 4:1. Mu/Ung<sub>3</sub> as 5:9. The dorsal surface of manubrium with many setae. The dorsal surface of the dens with coarse granules and seven setae situated just as in *H. manubrialis*. Mucro slightly curving and ending in a blunt head. A broad outer lamella runs from the base almost to the end of the mucro. The anal spines are small (although larger than those of *H. manubrialis*) and situated on subequal papillae. The spines are straight and pointed, while the papillae are slightly curved. The length of the spines plus the papillae subequal to Ung<sub>3</sub>. Body setae not well-developed. Distinction between Area Frontalis and Area Occipitalis slight. Th. II, III with m<sub>2</sub> missing; p<sub>4</sub> s.s. and longer than others; with a prominent fovea between p<sub>3</sub>-p<sub>4</sub>. Abd. I-III with setae in two rows; p<sub>5</sub> s.s. and larger than others; with fovea between p<sub>2</sub>-p<sub>3</sub> and proximal to p<sub>5</sub>. Abd. IV with setae in three rows and almost equal in length. Foveae proximal to p<sub>2</sub>, between m<sub>2</sub>-m<sub>3</sub> and proximal to p<sub>4</sub>, which is slightly larger than others. Abd. V with three rows of setae, m<sub>1</sub> being present; p<sub>3</sub> s.s. and longer than others. Abd. VI with setae in two rows.

This is the only species to have three rows of normal setae on abdominal segment V. In other features and particularly in the form of the mucro, it is akin to *H. manubrialis assimilis* Krausbauer. In one example, anal spines were lacking just as in *H. manubrialis* f. *neglecta* Born, 1900. In this case, an extra pair of setae (p<sub>1</sub>) were seen in the position of anal spines, implying that not only the unusual spines of *H. duplicispinosa* Yosii but also the normal anal spines are substantially equivalent to setae located in the same position. The species is named after my colleague, Dr. Kenneth Christiansen.

*Holotype*.—One male from Palouse, Washington, USA (K. Christiansen, collector).

*Paratypes*.—Four specimens from the same sample.

*Hypogastrura itaya* Kinoshita

Figs. 16, 62-68

Kinoshita, 1916.

Body length 1.2 mm. Pigment dark gray or bluish gray. Ventral side pale. Yellowish ground color seen along segmental margins and ventral side. Pigment distributed in patches. Ant./Head as 11:10. The ratio of antennal segments as 10:13:15:18. Ant. IV with a small end-bulb in a shallow groove with three to four socket setae. Sensory setae of dorsal side usually four in number and a little smaller than the normal setae. On the ventral surface near the end-bulb, one prominent, thick seta occurs. Third antennal segment organ normal and companion setae short and well-differentiated. Base of antenna not clearly separated from Area Frontalis. P.A.O. of four small elements. Whole organ is 1.5 times the diameter of one eye. Eyes eight per side upon black patches. Unguis with one inner tooth and often with one pair of lateral teeth. Unguiculus setaceous, half as long as the unguis,

with a small basal lamella. Tibiotarsus with tenent hairs 3, 4, 4 in number, well-developed and apically swollen. One dorsal tenent hair is slightly stronger than the lateral two which are inserted at the same level on the tibiotarsus. Middle and hind legs with an additional extra long tenent hair arising from a higher level of the tibiotarsus. This hair is absent on forelegs. Ventral tube with  $4 + 4$  setae. Rami of the tenaculum with three teeth. Furca slightly reduced, its apex reaching only to the foremargin of Abd. III. Manubrium with  $10 + 10$  setae on dorsal side. Dens ventrally smooth and dorsally finely granulated, with five setae, one external-basal seta being extra long.  $D/Mu$  as 3:1.  $Mu/Ung_3$  as 4:9. Mucro rather reduced, slightly curved and distally pointed, its outer margin being lamellate, with lobe at about the middle. Anal spines strongly recurved and acute. Basal papillae touching each other at the base and the margins between the papillae and the anal spines are higher in front than in back.  $An. sp./Ung_3$  as 1:3. Entire integument minutely granulated. Body setae not large, slightly thickened and truncate as in *H. viatica*. Area Verticalis confluent with Area Occipitalis and with  $2 + 2$  setae. Th. II, III with setae in three rows;  $p_2$  and  $p_4$  longer than others and slightly swollen at apex. Abd. V with setae in three rows; m-row ( $m_1$  and  $m_2$ ) very large and distally swollen, while those of a- and p-rows are normal. Abd. VI with two rows of setae.  $P_1$  and one lateral seta ( $p_2$ ?) very long and distally swollen. One other such seta present on the side-lobe of the anus.

Three rows of setae on Abd. V and clavate body hairs are characteristic of the present species.

*Specimens seen*.—Ten specimens from Mt. Kamuriki, Pref. Nagano (17 VI 1952, S. Ueno, collector); five specimens from Matsumoto, Pref. Nagano (18 VIII 1952, S. Ueno, collector).

#### THE RETICULATA GROUP

This group is characterized by s.s. assuming the position of  $p_4$ ,  $p_4$ ,  $p_4$ ,  $p_2$  upon Th. II, III, Abd. I-III, Abd. IV and Abd. V respectively. The only known species is *H. reticulata* Börner from Japan.

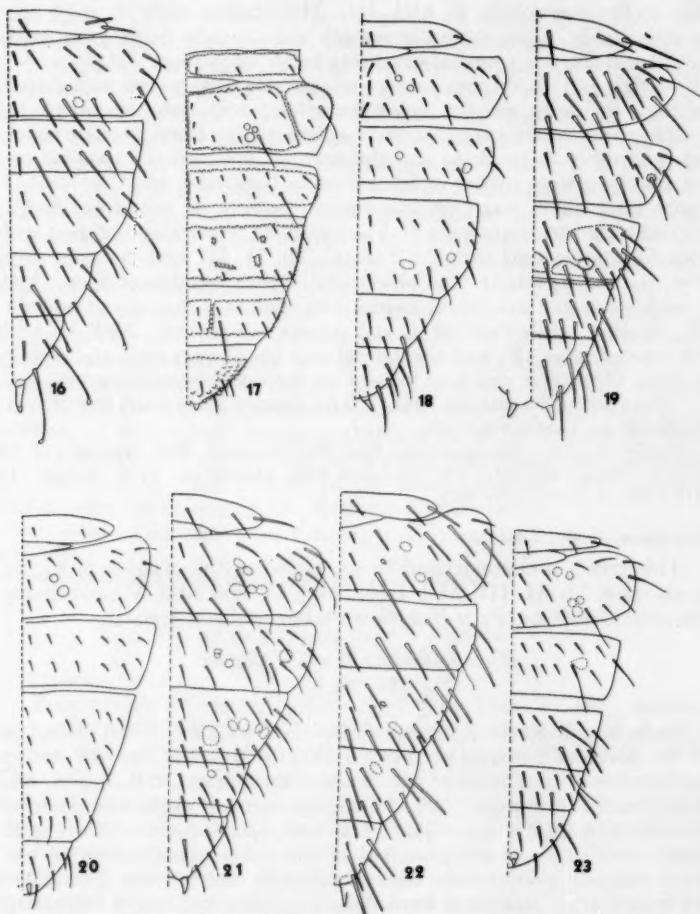
#### *Hypogastrura reticulata* Börner

Figs. 17, 46, 69-73

Börner, 1909.

Body length up to 2.3 mm. Color dark or black. Ant./Head as 25:30. Ratio of antennal segments I-IV as 3:5:5:12. Ant. IV with a small end-bulb in a shallow pit. Sensory setae blunt, rod-shaped, and more than 12 in number. Third antennal segment organ composed of two rods in a groove accompanied by two modified setae. Two additional modified setae are proximal to the latter. Anal antennal segments coarsely granulated. Base of antenna more finely granulated and thus sharply separated from Area Frontalis and Ant. I. Granulations extremely coarse on Area Ocularis. Eight eyes per side. P.A.O. small, with four oval elements in a shallow groove somewhat separated from Area Ocularis. One prominent tenent hair on each tibiotarsus which is not only longer than the unguis and very thick, but also dis-

tally enlarged in a triangular form as in the genus *Entomobrya*. Unguis with one distal inner tooth. Dorsal side strongly carinate; lateral tooth not observed. Unguiculus setaceous, about half as long as unguis and with a broad basal lamella. Ventral tube with 4+4 setae. Rami of the tenaculum with four teeth. Furca well-developed. Manubrium with about six setae dorsally. Dens minutely granulated dorsally and



Figs. 16-23.—16. *Hypogastrura* (*s. str.*) *itaya* Kinoshita. 17. *H.* (*s. str.*) *reticulata* Börner. 18. *H.* (*s. str.*) *manubrialis* (Tullberg). 19. *H.* (*s. str.*) *oregonensis* n. sp. 20. *H.* (*s. str.*) *nemoralis* n. sp. 21. (*s. str.*) *iwamurai* n. sp. 22. *H.* (*s. str.*) *viatica* (Tullberg). 23. *H.* (*s. str.*) *gracilis* (Folsom).

with seven setae including one elongated outer-lateral seta. D/Mu as 10:3. Mu/Ung<sub>3</sub> as 3:5. Mucro almost club-shaped, straight and distally rounded. Both sides of the mucro almost smooth, but sometimes with narrow lamellae, which may reach from the apex to the tip of the dentes or may vanish at about the middle. Anal spines minute, conical in profile, and on papillae which are as high as the spines and are confluent basally. An. sp./Mu as 1:2. Integument coarsely granulated as in *Odontella*. Head with Areas Frontalis and Verticalis coarsely granulated. Setae minute but still normal. One elongated fovea lies in the middle of the Area Frontalis and between t and c. A median band of clearly different granulation extends from the third abdominal segment to the Area Verticalis. Each segment has a coarsely granulated area at about the middle, sharply separated from the more finely granulated areas of the segmental margins. Th. II, III with m<sub>2</sub> apparently absent, only p<sub>4</sub> somewhat longer than the others and with two to three foveae nearby. Abd. I-III with two rows of setae; p<sub>4</sub> long and s.s. while the remaining setae are subequal and small. Abd. IV with setae in three rows; m<sub>2</sub> is apparently absent; a large fovea lateral to m<sub>1</sub> and p<sub>4</sub> very long and s.s. Abd. V with setae in two rows; posterior margin with a distinct finely granulated area; p<sub>2</sub> long and s.s. Abd. VI with setae slightly longer.

Our specimens agree well with the description of Börner, 1909, except for the P.A.O. which is not unilocular, but composed of four elements as usual.

*Specimens seen.*—The species appears frequently in great numbers in Central Japan during spring and autumn. Thirty specimens from Daimonji, Kyoto (20 XII 1953, R. Yosii, collector) and 18 specimens from Kasuga, Nara (9 III 1952, Y. Wada, collector).

#### THE MANUBRIALIS GROUP

Almost all species of *Hypogastrura* (s. str.) with 1, 1, 1 tenent hair on the tibiotarsus may be included in this group, although their chaetotaxy must be determined in each case. The position of s.s. upon Th. II, III, Abd. I-III, Abd. IV and Abd V is p<sub>4</sub>, p<sub>5</sub> and p<sub>3</sub>.

#### *Hypogastrura manubrialis* (Tullberg)

Figs. 18, 74-76

Syn. nov. *Achorutes yamagata* Kinoshita, 1916; *A. maturus* Folsom, 1919 (?).

Body length about 1.4 mm. Color grayish brown or bluish. Antennae deeply pigmented. Ventral side and extremities pale. Ant./Head as 1:1. Ant. IV with an extrusible end-bulb in a pit and some socket-setae near by. Sensory hairs in the form of long, somewhat curved rods, eight in number. Third antennal segment organ of two rods in a furrow and two modified setae. Unguis normal, with or without inner tooth about  $\frac{3}{4}$  distance from the base. Unguiculus two-thirds as long as unguis, setaceous, without lamella, but with one basal papilla. Tenent hairs long, 1, 1, 1 and acuminate or slightly knobbed at the end. Ventral tube with 4+4 setae. Rami of the tenaculum with

four teeth. Furca normal. Dens/Mu as 5:2. Dorsal surface of dens with coarse granulations and with seven setae including an outer basal seta longer than the others. In all the specimens which were examined, a slight thickening similar to a fold of skin can be seen just before the mucro. This is a diagnostic characteristic of the species. Mucro ventrally almost straight, slightly curved and rounded apically. An inconspicuous, very thin outer lamella is present. Anal spines minute and on small basal confluent papillae. These papillae are about three times as large as the normal skin granules and smaller than half or  $Ung_3$  in length. Body setae poorly developed and often invisible. Head with Area Verticalis confluent with Area Frontalis so that the 2+2 setae on the former seem to be  $d_1$  and  $sd_1$  of the latter. The furrow between Area Verticalis and Area Occipitalis can be either distinct or obscure. A pit lies between  $c_2$  and  $c_3$  as well as between  $p_3$  and  $p_4$ . Th. II, III with rather small setae; s.s. not differentiated. Abd. I-III with setae in two rows, those on both sides longer;  $p_5$  is s.s. and longer than all the others.

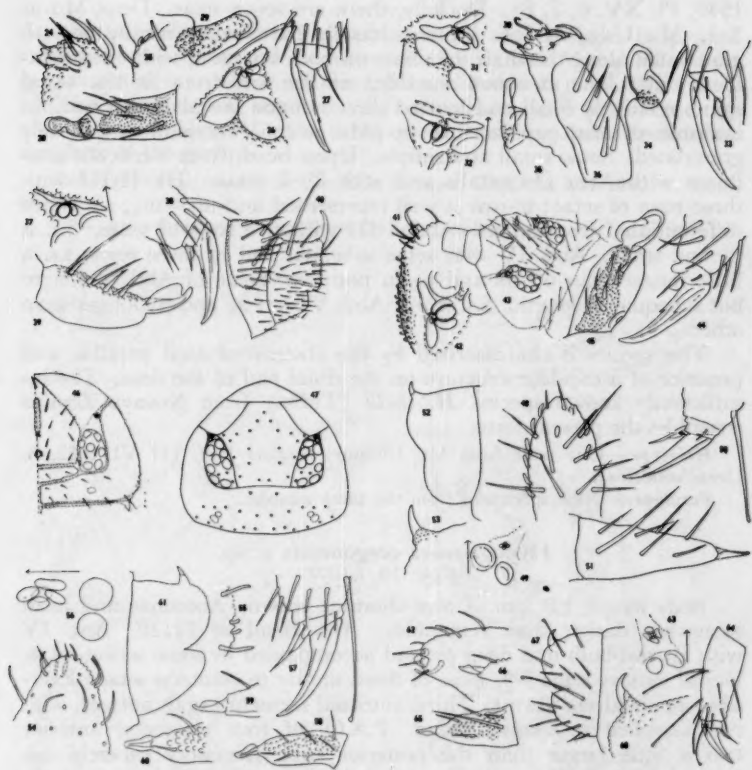
*Specimens seen*.—Thirty specimens from Otsu, Shiga Pref., Japan (29 X 1939, R. Yosii, collector); twenty specimens from Point Barrow, Alaska, USA (N. Weber, collector).

*Achorutes yamagata* Kinoshita from Japan is identical to this species. Material from Point Barrow includes many large and small specimens. Some of the specimens have a mucro of the type seen in *H. assimilis* with a broad lateral lamella and recurved apex. Their tenent hairs are usually clavate. There would seem to be no great difference between the present species and *H. assimilis*. The latter, therefore, cannot be regarded as a separate species.

#### *Hypogastrura nemoralis* n. sp.

Figs. 20, 77-83

Body length up to 1.8 mm. Whole body except furca brownish black. Ant./Head as 1:1. Ratio of antennal segments I-IV as 15:20:20:30. Ant. IV with an end-bulb in a shallow pit and some nearby socket hairs. Sensory setae long, somewhat curved, and 8 in number. Third antennal segment organ of two rods in a furrow accompanied by two modified setae. Base of the antenna not differentiated from Area Frontalis. Eyes eight per side. P.A.O. composed of four small elements. Whole organ equal to one eye in diameter. Between P.A.O. and Area Ocularis is a large tubercle which is apparently the accessory tubercle of P.A.O. Each tibiotarsus has one long tenent hair rounded at the tip. Unguis normal with one inner tooth at about the middle. Unguiculus setaceous, about half as long as the unguis and with a prominent, rounded basal lamella. Ventral tube with five setae per side. Rami of the tenaculum 4-toothed. The manubrium has only a few setae. A coarsely granulated area occurs on the dorsal surface of the dens about a quarter of the distance from the apex of the organ. Distal end of the dentes with a cap-like thickening of the integument just as in *H. bengtssoni* (Agren); (cf. Stach,



Figs. 24-68.—24-29.—*H. (Ceratophysella) pseudarmata* (Folsom). 24. Distal end of Ant. IV. 25. Ant. III-organ. 26. Postantennal organ. 27. Hind foot. 28. Dens and mucro (dorsal view). 29. Mucro. 30-36.—*H. (Cyclograna) vulgaris* n. sp. 30. Distal end of Ant. IV. 31. Postantennal organ. 32. Postantennal organ. 33. Hind foot. 34. Mucro (dorsal view). 35. Mucro (lateral view). 37-40.—*H. (Cyclograna) loricata* n. sp. 37. Postantennal organ. 38. Hind foot. 39. Dens and mucro. 40. Abd. V and VI (lateral view). 41-45.—*H. (Cyclograna) horrida* n. sp. 41. Ant. IV. 42. Postantennal organ. 43. Head capsule. 44. Middle foot. 45. Dens and mucro (dorsal view). 46. Chaetotaxy of the head of *H. (s. str.) reticulata* Börner. 47. Chaetotaxy of the head of *H. nivicola* (Fitch). 48-53.—*H. (s. str.) copiosa* (Folsom). 48. Ant. IV (dorsal view). 49. Postantennal organ. 50. Middle foot. 51. Dens and mucro (lateral view). 52. Abd. VI (lateral view). 53. Anal spine. 54-61.—*H. (s. str.) christianseni* n. sp. 54. Distal end of Ant. IV. 55. Ant. III-organ. 56. Postantennal organ. 57. Hind foot. 58. Dens and mucro (dorsal view). 59, 60. Mucro. 61. Abd. VI (lateral view). 62-68.—*H. (s. str.) itaya* Kinoshita. 62. Distal end of Ant. IV. 63. Postantennal organ. 64. Hind foot. 65. Dens and mucro. 66. Mucro. 67. Abd. VI (lateral view). 68. Anal spine (lateral view).

1940, Pl. XV, 6, 7, 8). Dorsally, there are seven setae. Dens/Mu as 3:1. Mu/Ung<sub>3</sub> as 5:6. Mucro dorsally flattened, ventrally curved, granulated along the shaft, laminate on both sides and with one prominent outer lobe at about one-third of the way from its tip. Anal spines relatively small and located directly upon the abdomen without intermittent anal papillae. An. sp./Mu as 1:5. Integument minutely granulated. Setae small and simple. Upon head, Area Verticalis confluent with Area Occipitalis and with 2+2 setae. Th. II-III with three rows of setae; m-row is well represented and  $m_2 = m_1$ ; s.s. is not differentiated from others. Abd. I-III with two rows of setae. S.s. is  $p_5$  and small. Abd. IV with setae subequal and in three rows; s.s. a little longer than others and  $p_5$  in position. Setae of Abd. V longer but subequal in length. S.s. is  $p_3$ . Abd. VI has  $a_1$  and  $p_1$  longer than others.

The species is characterized by the absence of anal papillae and presence of a cap-like structure on the distal end of the dens. The insufficiently known species, *H. thelli* (Tullb.) from Novaya Zemlya resembles the present form.

*Holotype*.—One male from Mt. Ubasute, Nagano Pref. (17 VI 1952, S. Ueno, collector).

*Paratypes*.—Nine specimens from the same sample.

#### *Hypogastrura oregonensis* n. sp.

Figs. 19, 84-89

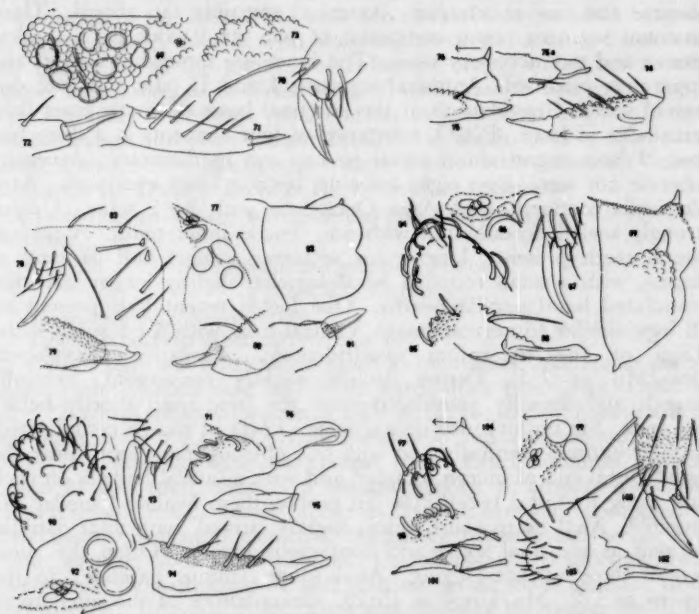
Body length 1.8 mm. Color chestnut brown. Antennae and head somewhat darker than remainder. Ant./Head as 12:10. Ant. IV with an end-bulb in a deep pit and accompanied by some socket-setae. Dorsal sensory setae 7-9, some of them similar to common setae. Ever-visible antennal sac absent. Third antennal segment organ normal, with two modified companion setae. P.A.O. of four elements; anterior two a little larger than the posterior two. Accessory tubercle not present. Eyes eight per side, upon black patch. Tibiotarsus lacks tenent hairs. Unguis with one inner tooth and a pair of lateral teeth. Unguiculus setaceous and with a very broad, rounded basal lamella. Ventral tube with 4+4 setae. Rami of the tenaculum with four teeth. Furca well-developed. Dens/Mu as 2:3. Dens dorsally coarsely granulated with seven setae. The granulation is more striking directly before the mucro, where the ventral side has a small cap-like thickening of the integument. Mucro laterally compressed and almost blade-like. Distally, there are two obscure teeth. Ventral side strongly carinate, with a small mucronal tunica near the base. Dorsally a small portion near the base is granulated. Anal spines about one quarter as long as the mucro. Basal papilla of the spine rather hemispherical, basally contiguous, and as high as the spines. Body setae simple and well-developed for the genus. All setae of Area Frontalis equally long. Area Verticalis with 2+2 setae and confluent with Area Occipitalis. Th. II, III with setae subequal;  $p_4$  is s.s. Abd. IV with a median, unpaired, coarsely granulated tubercle including  $p_2$  of both sides.

Another lateral tubercle with such a coarse area includes  $p_3$ - $p_6$  and extends anteriorly beyond the a-row.  $P_5$  is s.s. Abd. V and VI coarsely granulated over whole segment. Setae distributed normally.

The characteristic structure of furca, dentes, and mucro and the granulation of Abd. IV make the species at once separable from other members of the group.

*Holotype*.—One male from Corvallis, Oregon, USA (26 XII 1950, V. Roth, collector).

*Paratypes*.—Four specimens from the same sample.



Figs. 69-104.—69-73.—*H. (s. str.) reticulata* Börner. 69. Postantennal organ and eyes. 70. Middle foot. 71. Dens and mucro. 72. Mucro. 73. Anal spines (oblique dorsal view). 74-76.—*H. manubrialis* (Tullberg). 74. Dens and mucro (lateral view). 75, 75a. Mucro. 76. Anal spine. 77-83.—*H. nemoralis* n. sp. 77. Postantennal organ. 78. Hind foot. 79, 80, 81. Dens and mucro. 82. Abd. VI (lateral view). 83. Anal spines (oblique dorsal view). 84-89.—*H. oregonensis* n. sp. 84. Distal end of Ant. IV. 85. Ant. III-organ. 86. Postantennal organ. 87. Fore foot. 88. Mucro. 89. Abd. VI and anal spine (lateral view). 90-96.—*H. (s. str.) iwamurai* n. sp. 90. Distal end of Ant. IV (dorsal view). 91. Ant. III-organ. 92. Postantennal organ. 93. Fore foot. 94. Dens and mucro. 95, 96. Mucro. 97-104.—*H. (s. str.) gracilis* (Folsom). 97. Distal end of Ant. IV (ventral view). 98. Ant. III-organ. 99. Postantennal organ. 100. Middle foot. 101, 102. Mucro (lateral view). 103. Abd. VI (lateral view). 104. Anal spine.

*Hypogastrura iwamurae* n. sp.

Figs. 21, 90-96

Body length up to 2.5 mm. Body somewhat dorso-ventrally flattened as in *Ceratrimeria*. Ground color ash-gray. Dorsal side of the body and antennae bluish, other extremities pale. Ant./Head as 25:23. Ratio of antennal segments I-IV as 20:20:25:30. Ant. IV with a relatively small end-bulb in a deep groove, accompanied by some socket setae. More than 15 sensory setae on dorsal side, very long and distinctly curled at the apex. Peg-like setae of the ventral side obscure and few in number. Antennal eversible sac absent. Third antennal segment organ composed of two small rods in a shallow groove and two accessory setae. The latter are somewhat curved and apparently modified. Antennal segments I and II pale and with one row of setae. Granulations of the antennal bases distinctly finer than remainder of head. P.A.O. composed of four elements in a deep furrow. Whole organ about equal to one eye in diameter. Accessory tubercle not seen. Eyes eight per side, upon a black eye-patch. Area Verticalis confluent with Area Occipitalis with 2+2 setae. Unguis strongly keeled dorsally and with one central inner tooth. A pair of lateral teeth present. Unguiculus setaceous, about half as long as unguis, with a small rounded basal lamella, slightly longer than the granulated basal papilla nearby. One feeble tenent hair present on all legs, similar to normal setae. Ventral tube with 4+4 small setae. Rami of the tenaculum quadridentate. Furca well-developed. Dens/Mu as 7:3. Dentes distally slightly convergent, ventrally smooth and dorsally granulated from the base until shortly before the apex. Six unthickened dental setae. Form of mucro complicated, strongly carinate ventrally and with one obvious inner tooth near the base. Distal end of mucro rounded and with a lateral lamella on each side along its distal two-thirds. In profile, these hyaline lamellae are invisible. Anal horns short, thick, slightly curved, with anal papillae as long as the anal spine and contiguous basally. Often the spine reveals some surface ringing. Anal spines (minus papillae) to the mucro as 1:2. Mu/Ung<sub>3</sub> as 15:23. Granulations of the integument very coarse. Along the posterior margin of Abd. IV and V, there are a number of sharply delimited, finely granulated areas. Body setae long, simple and acuminate. The positions of s.s. on each of the body segments are as 0, 4, 4, 5, 5, 5, 5, 3, 0 in a posterior row. They are all subequal to the body setae.

This species is remarkable in the form of the mucro, and the sensory setae of the fourth antennal segment. The species name is dedicated to my friend, Michimasa Iwamura of Saikyo University.

*Holotype*.—One male from Asiu, Kyoto Pref., Japan (30 X 1937, M. Iwamura, collector).

*Paratypes*.—Three specimens from the same sample; fifteen specimens from Hyonosen, Hyogo Pref. Japan (28 VIII 1938, R. Yosii, collector); one specimen from Shizugadake, Shiga Pref., Japan (14 IX 1938, R. Yosii, collector).

## THE VIATICA GROUP

This group includes those species which usually have 2, 3, 3 tenent hairs on the tibiotarsus. Position of s.s. is normal.

*Hypogastrura viatica* (Tullberg)

Fig. 22

Tullberg, 1872; Stach, 1947.

Distribution of setae on head normal. Antennal bases undifferentiated. Area Verticalis confluent with Area Occipitalis and with 2+2 setae;  $v_1, v_2$ . Th. II, III with small fovea near  $m_2$  (lat.); s.s. is at the position of  $p_4$ . Abd. I-III with two rows of setae; a fovea between  $p_2$ - $p_3$ ;  $p_5$  is s.s.; Abd. IV with setae in three rows; a small fovea near  $m_2$  (lat.); s.s. at the position of either  $p_3$  or  $p_5$ , which are needle-shaped and subequal in form. Abd. V with setae in two rows. S.s. is  $p_3$ . The body setae show much variety in shape and length. Longer setae truncate and often serrate distally (see Stach, 1949); other setae small, simply needle-like in appearance. Dentes with six setae. Ventral tube with 4+4 hairs. Rami of the tenaculum tridentate.

*Specimens seen*.—Twenty-five examples from Liège, Belgium (F. Carpentier, collector).

*Hypogastrura gracilis* (Folsom)

Figs. 23, 97-103

*Achorutes gracilis* Folsom, 1899.*Achorutes tullbergi* Schaffer, 1900, syn. nov. (?)

Body length 1.5 mm. Color black to blue black. Antennae deeply pigmented. Ventral side and other extremities pale. Ant./Head as 10:9. Ratio of antennal segments I-IV as 12:13:18:30. Fourth antennal segment with a distal, trilobed end-bulb and a number of socket-setae. No peg-like setae on ventral side. Third antennal segment organ of two small rods in a shallow groove accompanied by two curved setae. P.A.O. small (about as large as one eye) composed of four minute, subequal elements. Accessory tubercle not seen. Eyes eight per side, upon black patches. Unguis of all legs subequal, relatively small, dorsally carinate and with one inner tooth near the distal end of each. Unguiculus setaceous and reaching three-quarters of the distance from base to apex of unguis. Basal half lamellated on the inner side with lamella apically arcuate ("lunate" of Folsom). Tenent hairs 2, 3, 3 rather thick and conspicuously swollen at apex; all of a given leg arise from the same level with the median seta slightly larger than others on mid- and hind legs. Dens/Mu as 3:1. Dentes almost smooth dorsally with seven setae. Mucro strongly compressed bilaterally and therefore somewhat blade-shaped. Apical tooth pointed, but anteapical tooth obscure and often absent. Mucro lamellate on both sides from the base to the anteapical tooth. Inner lamella not as conspicuous as outer one. Mu/Ung<sub>3</sub> as 10:11. Anal spine small and located on anal papilla as high as the spine itself and separated basally. Mu/An.sp. as 10:3. Integument minutely granulated. Body setae all very minute. Head with Area Verticalis confluent with Area Occipi-

talís and with 2+2 setae. Th. II, III with almost all setae equally long;  $p_4$  is s.s. and a little longer than others. Abd. I-III:  $p_5$  is s.s. about twice as long as other setae and located on the dorsal side of conspicuous fovea. Chaetotaxy of Abd. IV difficult to observe. At any rate,  $p_5$  is s.s. and longer than others. Abd. V with setae in two rows;  $p_2$  is smaller than  $p_1$ , and s.s.  $p_3$ .

The present species is very near to *H. tullbergi* Schaffer, 1900. The main difference is the shape of unguicular lamellae, which are arcuate in *gracilis* and rounded in *tullbergi*. It is by no means constant in form and I have found some examples with rounded lamellae and some intermediate forms between these extremes.

*Specimens seen*.—Thirteen specimens from the seashore near Hiroshima (Y. Taki, collector).

#### CONCLUSIONS

The crucial characteristic for separating *Ceratophysella* from *Hypogastrura* is the position of s.s. upon Th. II and III, and not the presence of an eversible antennal sac. With the former criterion it is possible to include in the genus cavernicolous forms such as *H. cavicola*, *H. troglodytes*, and *H. quinqueoculata*, all of which are obviously closely allied to *C. armata*.

Those species close to *Ceratophysella*, but having a peculiar P.A.O. form, and with s.s. at the position of  $p_4$  on the second and third thoracic segments are placed in the new subgenus *Cyclograna*. The members of this group exhibit a marked tendency toward "pluri-chaetosis" and "polychaetosis." Frequently some of the setae of the body are spine-like.

It is quite possible that all the forms here discussed are evolved from three species: *C. armata*, *C. communis*, and *C. vulgaris*. In terms of distribution these forms are European, Eastern Asiatic, and North American, respectively. Where they have given rise to cavernicolous forms, a number of troglobiontic species (*troglodytes*, *cavicola*, etc.) and even genera (*Typhlogastrura*, *Spelogastrura*, etc.) appear.

*Hypogastrura* (s. str.) is relatively difficult to subdivide and, except for the *nivicola* group, will require further study before any natural arrangement can be achieved.

#### ADDENDUM

Professor H. G. James of the Entomological Laboratory, Dept. of Agriculture in Belleville, Ontario, Canada, has kindly let me investigate the hypogastruran materials of his collection. With many thanks, I should like to note the results as follows:

#### *Ceratophysella armata* (Nicolet)

Many specimens from Geraldton, Ontario, Canada (12 IX 1933).

Many specimens from New Westminster, British Columbia, Canada (7 I 1949).

*Ceratophysella communis* (Folsom)

One specimen from Lampart House, Northwest Territories, Canada (20 VIII 1951).

One specimen from Rondeau Park, Ontario, Canada (2 X 1931).

Ten specimens from Pottageville, Ontario, Canada (3 IV 1931).

*Cyclograna vulgaris* Yoshii

Five specimens from Boyer, Oregon, USA (27 IV 1934).

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# The Physiology of Hunger in the Blowfly<sup>1</sup>

DAVID R. EVANS and L. BARTON BROWNE<sup>2</sup>

*Department of Biology, Johns Hopkins University,  
Baltimore 18, Maryland*

The behavior of an animal typically changes as a consequence of feeding and starvation, at least those aspects of its behavior that are adapted to the location and ingestion of food. The physiological basis of such changes has been long sought by vertebrate psychophysicologists, but the underlying mechanisms are still notably obscure. Of animals with simpler or more stereotyped behavior, similar questions have rarely been asked. Owing much to its usefulness in the study of chemoreceptor mechanisms, the blowfly is recently an exception. There have been a number of investigations directed at the mechanisms whereby feeding alters taste sensitivity, readiness to feed, control of intake, locomotor activity, and other behavior in addition to the abundant information regarding the properties of chemoreceptors as they are involved in feeding.

We have continued that line of investigation to fill in some of the gaps in the simple, rather thorough picture that has resulted. This paper gives the new evidence we have obtained (referred to herein as Evans and Barton Browne, unpublished), and attempts at the same time to evaluate other pertinent evidence and to present an integrated description of the physiology of hunger in the blowfly.

The use of the word "hunger" in the title requires some comment. It has been used there merely to connote those changes in behavior which are a consequence of feeding and starvation. The term has been avoided elsewhere in this paper in recognition of the difficulties engendered by its use. These difficulties are discussed later in order to make use of the experimental data in that discussion.

## FEEDING BEHAVIOR

In examining the effects of feeding and starvation on the feeding behavior of blowflies, we will consider first the effects on the behavioral threshold of the tarsal contact chemoreceptors and then, using the available data, we will discuss the mechanisms whereby ingestion is controlled. A discussion of the phenomenon of "hyperphagia," reported by Dethier and Bodenstein (1958), is also included.

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<sup>2</sup> Present address: C.S.I.R.O., Division of Entomology, Columbia, A.C.T., Australia.

## TASTE THRESHOLD

Feeding is known to decrease the sensitivity of flies to chemical stimulation in two ways. A short-term elevation of threshold is due to sensory adaptation, which Dethier (1952) has shown to be of two types, central and peripheral. Stimulation of a single chemoreceptor hair by a sugar solution soon adapts that receptor to the test solution but does not affect the response of other hairs to stimulation. When, however, many hairs are stimulated at once and for a prolonged period, the response to stimulation of still other hairs is blocked by adaptation of common elements farther along the reflex pathway. In addition, there is a long-term effect on the taste threshold caused by some action of the food after ingestion (Evans and Dethier, 1957).

We will deal mainly with this latter aspect.

## MEASUREMENT OF THRESHOLDS

The usual method of threshold measurement, that which was introduced by Dethier and Chadwick (1947, 1948), consists of determining the concentration of the test substance to which 50 per cent of a population of 120 flies exhibit a feeding response, i.e., extension of the proboscis. Two such thresholds generally must differ by threefold for significance at the one per cent level.

In order to work with smaller populations, we have devised a new method of treating tarsal thresholds. It can replace the usual methods only in those cases where a comparison of two or more thresholds on the same fly is part of the experimental design. Herein, we have used it to test the effect of some experimental treatment on the tarsal threshold to a given sugar. It can be used equally well to compare quantitatively the sensitivity of a group of flies to two or more compounds. While retaining the variability inherent in repeated tests on an individual, the method compensates for the variability among the members of the population, and thereby gives reliable results with fewer individuals. Ascending thresholds are obtained for individual flies, beginning at a concentration low enough that none of the flies will respond. After treatment another threshold is obtained for the same flies, beginning at the same low concentration. Since the series of test solutions is arranged as usual in doubling concentration steps, the second threshold of a fly must equal the first threshold  $\times 2^n$  where  $n$  is necessarily a whole number. To allow statistical treatment of cases where there is either no change in threshold or a decrease, the exponent is taken as the measure of threshold change. Thus, a negative exponent indicates a decrease; zero, no change; and a positive exponent, an increase. When a threshold is so high that no response occurs to a nearly saturated solution, e.g. 2 M glucose, it sometimes may be taken as being the next higher doubling concentration (4 M). The practice obviates discarding flies with the highest thresholds when the threshold obviously is high because of the treatment, and, if anything, errs in the direction of smaller-than-real differences. The mean value obtained

for the several flies may now be tested for the significance of difference from zero (e.g. Ostle, 1954); or two groups of flies may be given different treatments and the significance of the threshold changes compared in the two groups. Since significant results have been obtained with as few as 12 individuals, surgical or other laborious procedures are feasible as they would not be for populations of 120 flies.

#### CHANGES IN TASTE THRESHOLD AFTER FEEDING

The sensitivity of tarsal chemoreceptors to sugar (by behavioral test) is a function of the period of food deprivation; Figure 1 shows the glucose threshold measured as a function of time after a single ingestion of each of four sugars. The plots were made from the data of Evans and Dethier (1957). Curves of the same shape are obtained when fucose is used to measure threshold, but all threshold values are lower because fucose is slightly more stimulating than glucose (Hasset *et al.*, 1950). Fucose and glucose are highly stimulating to the tarsal and labellar chemoreceptors, mannose is weakly so, and lactose not at all. Fucose and lactose are not utilized by *Phormia* whereas mannose and glucose are excellent nutrients (Hasset *et al.*, 1950). Hence the ingestion of a sugar which is either non-stimulating, non-utilized, or both, is capable of elevating taste thresholds for some time after feeding. Arab (1957) has demonstrated that the sucrose thresholds of the labellar hairs individually and of the labellum as a whole are similar functions of feeding and starvation. Thus, it is probable that all of the external contact chemoreceptors which are involved in feeding behave similarly to one another in this respect. It should be noted, however, that the responses of the several chemoreceptor systems to less common sugars are not necessarily even of the same modality (Dethier *et al.*, 1956).

The early time-course of threshold elevation after feeding has been studied by Evans and Barton Browne (unpublished). Tarsal thresholds to glucose were determined 15, 25, and 45 minutes after feeding 2 M glucose. The 15 and 45 minute thresholds were not significantly different ( $p > 0.5$ ; mean  $n_{15-n_{45}} = -0.2 \pm 0.35$ ); but the threshold was less at 25 than at 45 minutes ( $p < 0.01$ ; mean  $n_{45-n_{25}} = 1.17 \pm 0.35$ ). This observation suggests that disadaptation (central and/or peripheral) is not complete by 15 minutes, contrary to the view of Evans and Dethier (1957).

#### THE EFFECTS OF THE VOLUME AND THE CONCENTRATION INGESTED ON THRESHOLD

Figure 1 shows that threshold changes are a function of the kind of sugar ingested. Evans and Barton Browne (unpublished) have examined the effect of altering the volume and the concentration of the solution ingested. Predetermined volumes of a sugar solution were transferred to a glass slide from a micropipette; a fly, mounted on a waxed stick by its wings, was allowed to feed on such a drop until a

TABLE I.—Tarsal thresholds to glucose after ingestion of fixed volumes and concentrations of glucose

Solution ingested	Mean initial threshold M glucose	n 15 minutes after feeding Mean $\pm$ S.E.	n 45 minutes after feeding Mean $\pm$ S.E.	Signifi- cance P
10 $\mu$ l 2 M glucose	0.135	3.5 $\pm$ 1.45	3.9 $\pm$ 1.24	) < 0.01
3 $\mu$ l 2 M glucose	0.175	1.8 $\pm$ 2.04	1.7 $\pm$ 1.57	
3 $\mu$ l 0.1 M glucose	0.238	0.2 $\pm$ 1.14	-0.3 $\pm$ 1.16	) < 0.01

negligible amount was left on the slide. Table I shows that 3  $\mu$ l of 2 M glucose raised the threshold significantly at both 15 and 45 minutes after feeding while 3  $\mu$ l of the 0.1 M solution did not. Ten  $\mu$ l of 2 M raised the threshold by a significantly greater amount than did 3  $\mu$ l of the same concentration. Thus, both volume and concentration of the ingested solution by some mechanism influenced the level to which taste threshold was elevated.

#### THE EFFECT OF THE INGESTION OF PROTEINACEOUS FOODS ON TASTE THRESHOLD

Blowflies readily feed on meat and other proteinaceous materials. Evans and Barton Browne (unpublished) have examined the effect of the ingestion of liver on taste threshold to glucose. The glucose thresholds of flies which had been allowed to feed to repletion on whole liver for 30 minutes were tested an hour after the termination of feeding. Their thresholds were found to be as high (mean threshold of 18 flies was 2.7 M) as those of flies fed to repletion on 2 M glucose (Fig. 1).

#### THE CONTROL OF THRESHOLD

The action of the sugar solution on the external chemoreceptors (i.e., adaptation) is too brief to account for the prolonged elevation of threshold after feeding (Evans and Dethier, 1957). Nor, as Dethier and Bodenstein (1958) have shown, does the mere performance of the ingestive act affect thresholds to sugars. Thus, the threshold-elevating action of the ingested solution must be internal. All but a small volume of an ingested solution is diverted into the crop. A constriction of the crop duct near its orifice into the esophagus and peristaltic waves toward the crop contain the sugar solution in the crop. For several days after ingestion of a concentrated solution of a "sweet" sugar to satiety, the crop duct and cardiac valve periodically act in unison to pass a discrete "slug" from the crop to the midgut, where absorption takes place. This transfer is very rapid and occurs with little if any loss of the solution in the esophagus.

Two alternatives, the first, that the ingested solution acts after absorption, and the second that it acts in some region of the gut, have been extensively explored. The evidence which favors the second pos-

sibility will now be presented and the possibility of a hormonal link in the chain of events leading to elevation of the threshold will be evaluated.

*Action after absorption.*—The immediate result of the absorption of sugars from the gut is an increase in the concentration of sugar in the blood. In the case of utilizable sugars, this is accompanied by a change in the metabolic state of the tissues as the sugar is taken up from the blood. The fact that feeding on fucose and lactose, which are not utilized, causes flies to become less responsive to sugars, argues strongly against any possibility that the metabolic state of the tissues has any influence on taste thresholds.

Evans and Dethier (1957) determined sugar concentrations in the blood of flies after feeding and found no consistent relationship between the taste threshold and either the total blood sugar or the concentration of any single sugar. They also found that injection of large amounts of sugar into the haemocoels of starved flies had no effect upon taste thresholds. Under more natural circumstances blood sugar and threshold were again dissociated; Evans and Dethier (1957) found that blood sugar levels increased during a recuperation period following prolonged flight, although the threshold remained low. In view of these several unsuccessful attempts to demonstrate an action of sugar after absorption, it seems very likely that the threshold-regulating mechanism is located in some region of the gut.

*Action in the digestive tract.*—Since the crop empties over a period of days (Evans and Dethier, 1957), the sugar solution is present in the digestive tract for a period similar to the period of threshold elevation (Fig. 1). However, a number of experiments eliminate the crop itself as the site of action. When crop volume was plotted against glucose threshold for each of the sugars tested, no consistent relationship was apparent (Barton Browne and Evans, 1960). More directly, ligation of the crop duct (Evans and Dethier, 1957), or even removal of the crop (Dethier and Bodenstein, 1958), did not prevent threshold elevation although the period of elevation was diminished. The volume ingested was, of course, much less after ligation of the crop duct, and ligation of the duct after feeding left only a small volume of the ingested solution in the foregut and midgut. It seems unlikely that these small amounts of sugars would remain long in the digestive tract of otherwise starved flies; but threshold remained elevated for 4 hours or slightly longer, an observation which may indicate a lag in the decline of the threshold after the gut is empty. Introduction of sugar into the midgut by injection or by enema did not elevate the threshold (Dethier and Bodenstein, 1958). Hence, these regions do not appear to be involved. Furthermore, these experiments constitute additional evidence against an internal action of sugar, since they must have duplicated at least qualitatively most of the effects of feeding, everywhere but in the foregut. Again pointing to the foregut as the site of action was the demonstration that a ligature just behind

the proventriculus did not prevent threshold elevation when a sugar solution was fed (Dethier and Bodenstein, 1958). All of the above results argue, largely by the elimination of other possibilities, that the threshold-regulating mechanism is located in the foregut exclusive of the crop. From other evidence, Arab (1957) has postulated the existence in the foregut of chemoreceptors which could possibly be involved.

One direct test of the involvement of the foregut has been reported: Dethier and Bodenstein (1958) cut the recurrent nerve just anterior to the corpus cardiacum and by so doing produced "hyperphagic" flies. This result was interpreted to mean that severing the innervation of the foregut via the recurrent nerve interrupted the neural pathway of foregut receptors, the response of which to ingested solutions normally elevates taste thresholds. Unpublished experiments by Evans and Barton Browne that do not support this interpretation are discussed below, together with other aspects of the problem of "hyperphagia." At this stage we regard the relation between input via the recurrent nerve and taste threshold as not satisfactorily demonstrated.

For convenience, we have stated throughout that the ingestion of sugar solutions elevates taste thresholds. This usage, however, ignores the possibility that it may be the absence of solutions in the foregut which causes a sensory input (as, for example, the hunger contractions of the human stomach). If cutting the recurrent nerve does not prevent threshold elevation, then there does not seem to be any compelling reason to prefer the one hypothesis to the other. The input from the foregut might therefore be inhibitory or excitatory in the central nervous system and might be evoked by either the presence or the absence of solutions.

*The possibility of a hormonal link.*—Two characteristics of the time course of taste threshold after feeding suggest that there may be a hormonal link in the chain of events causing threshold elevation. First, there is the slow attainment of peak threshold. There is a lag of between one and six hours, depending on the sugar used (Fig. 1). Secondly, there is the surprisingly long period of threshold elevation which occurs after feeding of flies, the crops of which have been well ligated or removed (discussed above). Also, de Wilde (1958) has shown that the corpus allatum is intimately involved in the feeding behavior of the Colorado potato beetle. Dethier and Bodenstein (1958) reported that the transfer of diluted blood from fed to starved flies, and the reverse, had no effect on taste threshold. This result argues against the existence of a hormonal link but must be treated with reservation, since any hormone present would have been diluted.

*Conclusions.*—The relationship between feeding and taste threshold may be summarized by saying that the ingestion of sugars and liver elevates the taste threshold and that the site of action of these substances on the threshold-controlling mechanism appears to be in

the foregut. The actual mechanism involved, however, remains virtually unknown.

#### THE CONTROL OF INGESTION

The act of feeding in the blowfly may be discussed in terms of a sequence of events: feeding is initiated, maintained, and terminated. It proceeds at a certain rate. This rate and the duration of feeding determine the quantity of food ingested.

#### INITIATION OF FEEDING

Initiation of feeding involves extension of the proboscis, spreading of the labellar lobes, and the commencement of sucking. All three processes may be elicited by the application of an adequate, acceptable stimulus to one or more of the tarsal or labellar chemosensory hairs. This may be demonstrated by stimulating tarsal or labellar hairs in a way that prevents ingestion of the test solution; under these conditions a fly, dissected to expose its foregut, may be observed to swallow bubbles of air. Normally, however, other sets of receptors are also involved. Spreading of the labellar lobes brings the interpseudotracheal papillae into contact with the stimulating solution. These, like the other contact chemoreceptors, influence feeding. While the tarsal and labellar hairs appear to have the same spectrum of acceptable and unacceptable compounds and a similar threshold (Arab, 1957), evidence has been presented that the papillae reject some compounds that are acceptable for the hairs and have lower thresholds for others than do the hairs (Dethier *et al.*, 1956). In addition, there are indications that

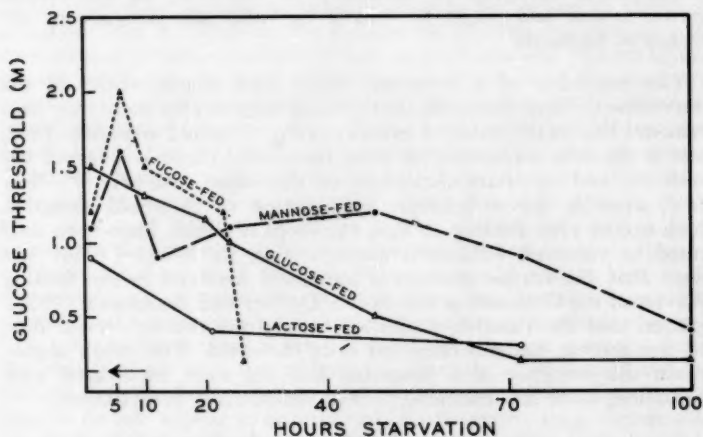


Fig. 1.—The effect of a single feeding on each of four sugars upon subsequent tarsal thresholds to glucose. The arrow indicates the average pre-feeding threshold to glucose (data of Evans and Dethier, 1957).

chemoreceptors, located in the pharynx or esophagus, also monitor injection (Arab, 1957). Feeding is a function of the kind and quantity of input of all these receptor populations.

Only water and some carbohydrates among the pure compounds tested have proven to be acceptable stimuli. A variety of chemically complex, natural foodstuffs are acceptable, but the chemicals responsible are unknown. Bending of the chemosensory hair in extreme starvation can evoke extension of the proboscis; this response has been shown to be mediated by a mechanoreceptor neurone associated with the hair socket (Wolbarsht and Dethier, 1958).

The odor of some foodstuffs attracts blowflies, but the effect of these odors on proboscis extension and ingestion has been little studied. While beef liver is readily ingested by *Phormia*, its odor seems unimportant. Evans and Barton Browne (unpublished) observed that tarsal contact was necessary to elicit proboscis extension and that the response was unaffected by removal of the antennae and palps, which are known to bear the principal olfactory receptors (Dethier, 1954).

#### CONTROL OF THE AMOUNT OF FOOD INGESTED

*Duration of feeding.*—The duration of active ingestion of a solution appears to be a function of the stimulating effectiveness of the solution and of the taste threshold of the fly. The duration of feeding is greater on the higher concentrations of a given sugar (Dethier *et al.*, 1956), concentrations which naturally are more stimulating. Evans and Barton Browne (unpublished) have demonstrated, in two experiments, that a relationship exists between the taste threshold and the duration of feeding. Flies were fed to repletion on 0.1 M sucrose solution and were then starved. At intervals from 24 to 72 hours after feeding, batches of these flies were fed 1 M sucrose solution and the

TABLE II.—Duration of feeding on 1 M sucrose as a function of starvation

Hours starvation	Duration of feeding (sec.)
	Mean $\pm$ S.E.
24	51 $\pm$ 4.2
36	66 $\pm$ 4.8
48	72 $\pm$ 3.0
60	86 $\pm$ 1.6
72	133 $\pm$ 7.9

TABLE III.—Feeding duration on 2 M glucose after ingestion of 2 M glucose and 2 M mannose

Treatment	No. of flies	Feeding duration (sec.) 1 hour after feeding	Feeding duration (sec.) 3 or 4 hours after feeding	Signifi- cance P
		Mean $\pm$ S.E.	Mean $\pm$ S.E.	
Glucose-fed	29	5 $\pm$ 0.53	19 $\pm$ 3.3	< 0.001
	26	9 $\pm$ 1.3	35 $\pm$ 3.1	< 0.001
Mannose-fed	44	5 $\pm$ 0.2	4.0 $\pm$ 0.4	> 0.05

duration of feeding recorded. Table II shows that the duration of feeding increased with the period of starvation. In the second experiment flies were fed to repletion on 2 M glucose or 2 M mannose. The flies fed 2 M glucose were again fed this solution 1 hour and 3 hours after the initial feeding and the durations were measured. The flies fed the mannose solution were similarly tested with 2 M glucose 1 and 4 hours after the initial feeding. Table III shows that the feeding durations were roughly correlated (negatively) with the taste thresholds shown in Figure 1 for flies fed on these sugar solutions. For flies fed on 2 M glucose the taste threshold decreases in the time interval between 1 and 3 hours after feeding, and it was found that the feeding duration increased during this period. The taste thresholds of flies fed 2 M mannose increased between 1 and 4 hours. Duration of feeding for flies fed on this sugar remained about the same during this period and perhaps even decreased slightly. The observation of Dethier *et al.* (1956) that ligation of the crop duct does not affect the duration of feeding excludes the possibility that gut capacity plays any part.

On the basis of these observations Dethier *et al.* (1956) postulated that an adequate, acceptable chemosensory input is necessary to maintain the sucking response and that ingestion continues as long as the solution tastes "sweet", i.e., until peripheral and central adaptation proceed to a level which renders the solution effectively tasteless. This view does account for the data, and the data exclude a number of other possibilities. The only assumption required is that adaptation to a given level takes longer with more intense stimuli, and this, of course, is quite generally true of sense organs. Implicit in the concept of a threshold-regulating mechanism is that it act somewhere along the reflex chain for proboscis extension in an appropriate manner; such an action would necessarily add with adaptation.

*Rate of intake.*—The mean rate of intake of sugar solutions has been calculated from measurements of intake volume and duration (Dethier *et al.*, 1956). Generally, rate appears related to the "sweetness" of the solution, to the quantity of acceptable chemosensory input. Sensory input, wherever it has been examined, tends to follow the Weber-Fechner rule, the magnitude of response being proportional to the logarithm of stimulus intensity (e.g. Granit, 1955). Typically, deviations occur at extreme intensities where response increases less rapidly with intensity. The behavioral data of Dethier and Rhoades (1954) show that the Weber fraction (just-noticeable-differences) of preference for sugar solutions by *Phormia* exhibits the typical U-shaped relationship to concentration (Fig. 2). And electrophysiological studies in progress (Evans, unpublished) demonstrated that single chemoreceptor neurones in the hairs exhibit the familiar stimulus intensity-response relationship; a plot of initial frequency of response against log concentration is sigmoid with a long linear segment at intermediate concentrations. The few rate measurements available (Dethier *et al.*, 1956) are in accord with this view; rate of intake increases uniformly with log concentration and declines at near-saturated

concentrations. This, however, cannot be the whole explanation, for rate in certain cases is actually less at the highest concentration than at some lower concentration. Another factor must be involved at the highest concentrations.

Viscosity is one obvious possibility, since concentrated solutions of sugars are notably viscous. The viscosity of sucrose solutions does vary in a way that is roughly appropriate (Fig. 2; data calculated from Bates *et al.*, 1942); viscosity increases rapidly at about 1 M, the concentration at which ingestion rate begins to decline. Dethier *et al.* (1956) demonstrated that viscosity does, in fact, have an effect on the rate of intake. Glycerol, which is tasteless for the blowfly, or nearly so, when added to sucrose solutions markedly decreased the rate of intake but did not affect duration. The rate of intake of a glycerol — 1 M sucrose solution with a viscosity of approximately 50 cp was slightly less than on a 2 M sucrose solution which has a similar viscosity and is slightly more stimulating than the 1 M solution.

Back pressure from the crop or abdomen probably does not normally play a significant part in hindering intake. Normal flies take in about half as much as do the "hyperphagic" flies, the feeding of which is discussed below.

*The volume intake of beef liver.*—Evans and Barton Browne (unpublished) determined the weights of the crops of flies which had been

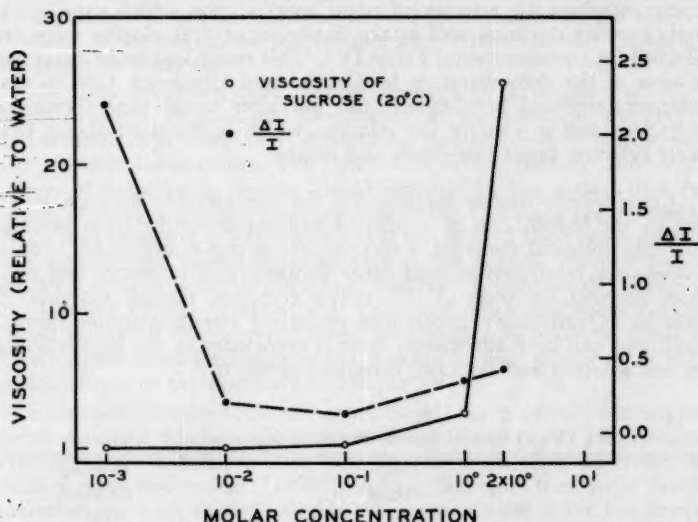


Fig. 2.—Continuous line: viscosity of sucrose solutions as a function of concentration (calculated from data in Bates *et al.*, 1942). Dashed line: ability of the blowfly to detect concentration differences as a function of concentration (data of Dethier and Rhoades, 1954).

allowed access to fresh, whole liver for 1 hour. The mean crop weight was found to be 25 mg. This compares favorably with the crop weight of flies allowed to feed under similar conditions on highly stimulating sugar solutions such as 2 M glucose. In addition, it was found that removal of the antennae and palps did not reduce the intake of liver. Liver appears, therefore, to be highly stimulating for at least one of the contact chemoreceptor systems; removal of the principal olfactory receptors did not markedly influence intake. The intake is almost certainly higher than would be expected if the mono- and oligosaccharide content of the liver were solely responsible and is taken as evidence that other components of liver, not yet tested in pure form, are stimulating to the contact chemoreceptors. The finding that flies which have been fully adapted to liver will respond to 1 M sucrose and that the reverse is not the case shows that the tarsal receptors are less stimulated than would be expected from the volume intake and indicated that other contact receptors, therefore, are more responsive.

*Intake of sugar solutions after removal of antennae.*—A number of investigators have reported experiments which seem to indicate inhibitory effects (possibly spontaneous) of receptor-bearing structures. Removal of palps or antennae released some activity as if they normally were active and inhibitory. Dethier (1953), for example, has shown that extirpation of the olfactory receptors of lepidopterous larvae increases the number of plant species upon which they would feed. Feeding duration and intake, however, of 2 M glucose were not affected by antennectomy (Table IV). This result was to be expected, in view of the demonstration by Dethier and Chadwick (1947) that antennectomy and labellectomy did not alter tarsal taste threshold; to sucrose and in view of the relation, which is discussed above, that exists between tarsal thresholds and intake.

*Conclusion.*—Rather surprisingly, the considerable data on ingestion by the blowfly can be explained without departing from familiar neurophysiological concepts. Receptor and synaptic adaptation, stimulus-response relationships, and other properties of receptors and neurones account for most of this rather complex, though stereotyped, behavior. Quantitative predictions regarding ingestion under normal conditions can be made merely from a knowledge of the properties of the test solution and the taste threshold of the fly.

TABLE IV.—Effect of antennectomy on ingestion of 2 M glucose

	Crop weight (mg) Mean $\pm$ S.E.	Feeding duration (sec.) Mean $\pm$ S.E.
Normal	15.6 $\pm$ 2.0	58.7 $\pm$ 7.3
Antenna-less	18.0 $\pm$ 2.5	77.0 $\pm$ 11

)  $P > 0.4$

)  $P > 0.1$

## HYPERPHAGIA

Dethier and Bodenstein (1958) cut the recurrent nerve of *P. regina* just anterior to the corpus cardiacum and, by so doing, produced hyperphagic flies. They interpreted this result to mean that cutting the recurrent nerve interrupted the neural pathway to the brain from unidentified receptors in the foregut, the stimulation of which by ingested solutions normally elevates the taste threshold. This interpretation was supported by the observation that flies made hyperphagic on a 1 M sucrose solution responded, after they had disadapted, to a 0.1 M solution. However, some criticisms of these experiments and their interpretation may be made:

- (1) No quantitative criterion of hyperphagia was given.
- (2) All tests were performed on sucrose solutions. There are no published data regarding the effect of ingestion of this sugar on subsequent taste thresholds.
- (3) The method of feeding departed from the usual in that flies were left in contact with the sucrose solution for long periods or were given repeated opportunities to feed. Especially because sucrose is among the most stimulating sugars for the blowfly, the quantities ingested would be expected to be considerably greater than normal.
- (4) Dethier and Bodenstein (1958) stated that cutting of the recurrent nerve prevents emptying of the crop. If this is so, any failure of taste threshold to rise could just as well be explained by the absence of sugar in the region of the foregut which contains the threshold-regulating mechanism.
- (5) The operation may involve damage to a number of other tissues (muscles, air sacs, and esophagus). In its execution, the corpus cardiacumallatum complex is denervated and handled. Recently, several workers have shown that hormones affect feeding and other aspects of behavior in insects. De Wilde (1958) has shown that the corpus allatum is necessary for feeding in the Colorado potato beetle. Ozbas and Hodgson (1958) found that extracts of the corpus cardiacum reduced the spontaneous activity of the central nervous system and locomotor activity in the roach *Blaberus*. Subsequently, Hodgson and Geldiay (1959) reported that operative shock and other trauma caused release of this material from the gland. Any observed effect of the recurrent nerve sectioning could possibly be due, wholly or in part, to side effects of the operative technique.

Evans and Barton Browne (unpublished) have carried out experiments designed to throw light on some of these points of criticism. The operative technique used was the same as that described by Dethier and Bodenstein (1958), except that the flies were briefly anaesthetized with carbon dioxide during preparation for the operation and testing. (We are indebted to Dr. Bodenstein for instructing us in the method of this difficult operation.)

The recurrent nerves of 48 flies taken from groups of standardized (24 hour starved) flies were sectioned. Others of the groups were given

sham operations which consisted of opening the neck membrane and proceeding with the operation until the corpus allatum-cardiacum complex was visible. Still others were kept as unoperated controls. All the flies were mounted on waxed sticks for testing. One hour or more after the operation and mounting, ascending thresholds to glucose solutions were obtained for all flies. In general these thresholds were greater for the two operated groups than for the controls. Those flies which did not respond to a 0.5 M solution were discarded. Next, all flies were fed once on a 2 M glucose solution until feeding ceased. One hour later glucose thresholds were again obtained. It was found that the thresholds of all three sets of flies at this time were similar. No fly responded to a concentration of less than 1 M and many in each group failed to respond to a 2 M solution. All flies were then fed repeatedly from a brush dipped in 2 M glucose; 15 of the flies which had had their recurrent nerves sectioned became hyperphagic. Only flies found, at the end of the experiment, to have crop weights of 50 mg or more were considered to be hyperphagic. No flies in either the control or sham operated sets were found to have a crop weight above 40 mg. The ascending thresholds of all flies which had sectioned recurrent nerves were repeatedly measured. All had high thresholds, and the hyperphagic ones especially so. None of these responded to 2 M glucose even if allowed both tarsal and labellar contact.

To ascertain that the use of the ascending method of determining thresholds did not give falsely high thresholds, the flies were tested by transferring them directly from water to the 2 M solution without contact with the lower concentrations. Similar results were obtained by this method.

Tarsal thresholds to sugar solutions can only be obtained after the tarsal chemoreceptors have been adapted to water. Hyperphagic flies often were found to have an abnormal response, in that they repeatedly responded to water alone. Because of this it was necessary to retest the response of each fly to water after it had given a positive response to a sugar solution so as to verify that the response was, in fact, to sugar. We feel that the abnormal water response might be involved in explaining the discrepancy between our results and those of Dethier and Bodenstein (1958), in that the persistent hyper-sensitivity to water would tend to mask any elevation of the sugar threshold.

No direct investigation was made of the possibility that damage to some organ other than the recurrent nerve might have been involved in the production of hyperphagia. Both of us did, however, gain an impression that the neatest operations were not the ones that gave rise to hyperphagic flies. Unfortunately, we were unable to devise an appropriate control operation to test this impression. A small-scale experiment was carried out to test the assertion made by Dethier and Bodenstein (1958) that flies with sectioned recurrent nerves are unable to pass sugar from the crop into the foregut and thence through the cardiac valve into the midgut. The recurrent nerves of a number of flies were cut and the flies given repeated opportunities to feed on

2 M glucose. Those which became hyperphagic were allowed to remain mounted on wax sticks. Most of them survived for more than 2 days and even after only one day were no longer bloated. Repeated feeding at any time caused these flies to become hyperphagic again. Since absorption occurs only in the midgut (Evans and Dethier, 1957; Hudson, 1958), it is clear that sugar solution must have passed from the crop into the midgut. Additional evidence for emptying of the crop is that hyperphagic flies were frequently observed to regurgitate.

If cutting the recurrent nerve does in fact lead necessarily to hyperphagia, explanations other than interference with threshold regulation are possible. For instance, although crop distension probably play no part in the control of ingestion when a normal volume is ingested (Evans and Dethier, 1957; Dethier and Bodenstein, 1958), intake, especially the rate and pumping force, might well be influenced by sensory input from the crop when the crop and abdomen are distended by two or three times their normal maximum volume. The force of distension was sufficient on occasion to rupture the abdominal wall.

In view of the evidence available, we conclude that some aspect of the operation did upset the mechanism controlling the intake of food in such a way as to allow hyperphagia to occur. We feel, however, that the mechanism involved has not yet been satisfactorily demonstrated and that threshold regulation probably is not altered by the operation.

#### LOCOMOTOR ACTIVITY

Locomotor activity is another aspect of the behavior of *P. regina* which is influenced by feeding and starvation (Barton Browne and Evans, 1960). Flies starved for 24 hours were found to be at least 4 times more active than those fed to repletion on strong sugar solutions. Feeding on the non-utilizable sugar fucose was even more effective in reducing activity than was feeding on glucose. Hence, as is the case with taste threshold, the metabolic state of the tissues is not the determining factor. Blood sugar concentration was also eliminated as a possible determinant by the observation that fucose-fed flies were fully active 27 hours after feeding, at which time their blood sugar concentration was very high. It was found that locomotor activity increased steadily with time after feeding on either glucose, mannose, or fucose, whereas the threshold increased to a peak some hours after feeding when flies were fed either of the latter two sugars (Fig. 1). Hence taste threshold and activity are not well correlated and bear different relationships to one another in flies fed different sugars. This finding is interpreted as evidence that the mechanisms by which the ingestion of sugar controls threshold and locomotor activity are not identical. Locomotor activity seems best correlated with crop volume and hence with the rate of emptying of the crop. Injection of water into the haemocoels of flies greatly reduced their activity. This result suggests that dilution of the blood may have been the ultimate factor determining locomotor activity after feeding.

## ECOLOGICAL ASPECTS

Any attempt to apply the available data on the changes in threshold and locomotor activity after feeding to feeding behavior under natural conditions is hampered by the paucity of information about the normal feeding habits of even the major species of blowflies. It seems safe, however, to generalize that most adult blowflies feed on nectar, honeydew, and decaying materials, especially carrion. It is first of interest to know the concentrations of sugar solutions available in nature. Hocking (1953) lists a number of species of plants as having nectar consisting of sugar solutions of a very high concentration, some even exceeding 70 per cent sugar. In most nectars sucrose, glucose, fructose, and less commonly, maltose, are present (Wykes, 1952). Certain nectars would, therefore, be extremely stimulating. Honeydew is known to contain the stimulating sugars fructose, glucose, and sucrose (Gray and Fraenkel, 1954), and whatever its concentration at the time of its production, evaporation would soon increase this. Results given in this paper indicate that the crops of flies that feed on meat can be as full as those of flies that feed on highly stimulating sugar solutions and that meat ingestion raises the sugar threshold to a high level. The situation may be summarized by saying that the flies have access to many sources of food, that many of these are highly stimulating, and that large amounts of them would be ingested if encountered. In nature, therefore, the flies are confronted with a complex "preference-aversion" situation. In this type of situation it has been shown that when flies are given a choice of two acceptable solutions, one of which is more stimulating than the other, almost all feeding is on the more stimulating one (Dethier and Rhoades, 1954). The same result would be expected in nature in places where there is an abundance of food. This is borne out by the observation of Hocking (1953) that many specimens of blood-sucking insects which had been caught in the field had highly concentrated sugar solutions in their crops. Only under conditions where the supply of food was inadequate would ingestion of the less stimulating solutions be expected.

Barton Browne and Evans (1960) have shown that the locomotor activity of *Phormia regina* falls to a low level after the flies have fed to repletion and steadily increases again with starvation, and that the level of activity is a function of the volume of the crop. This means that flies, after a small period of almost complete inactivity immediately after feeding to repletion, begin to move and hence encounter food, and that the frequency of encounters would increase as the flies became more starved. Although the activity of flies which had ingested smaller than normal amounts was not tested, it is highly probable that these do not become as inactive as flies which have fed maximally.

Evans and Dethier (1957) demonstrated that the taste threshold of *P. regina* fed to repletion on any one of a number of sugars, was never so high that a large percentage of the flies failed to respond to the highest concentrations of sugars. For instance, flies fed to repletion on 2 M glucose have a mean threshold to glucose of 1.5 M; hence

more than half of them were able to respond again to 2 M glucose as soon as disadaptation had occurred, even though threshold was maximal. Furthermore, it has been shown above that, at least for flies fed 2 M glucose, feeding duration, and therefore, probably, the volume intake of 2 M glucose, increased with time after feeding, and by 3 hours had become quite appreciable. It is clear from these results that flies are able to make use of encounters with highly stimulating solutions even a short time after feeding to repletion. Other experiments described above indicate that the level to which the threshold rises depends on the volume and the concentration of the sugar ingested. Hence, a fly which is interrupted in its feeding, or which feeds on a solution which is not highly stimulating, would immediately be able to respond to and probably imbibe appreciable quantities of the more stimulating solutions.

It is apparent that control of locomotor activity and food intake, after feeding, work in harmony in *Phormia*, in that the chance of encountering food increases as the fly becomes more and more able to take in more food. These mechanisms, working together, would tend to keep the flies in nature continuously more or less fully fed in areas where food materials are abundant.

The role of odor is difficult to assess. Apparently nutritional state as a variable in studies of attractants and repellents has not received much attention. One might expect that fed animals would be less responsive to attractants than starved, and such a result has been reported for mosquitoes (Christophers, 1947).

However, the primary effect of feeding might be on locomotor activity, rather than responsiveness to the odor *per se*. Odor certainly attracts flies to decaying materials, but data reported above suggest that the odor has no effect on the intake of liver by blowflies. Some species of blowflies are reported to feed on flowers with fetid or carrion-like odors (Hall, 1947). In these cases, it is not known whether the odor acts only as an attractant or whether it also acts as a feeding stimulant. In this latter case, one must distinguish between odors which evoke extension of the proboscis and those which augment intake of a test solution, since some that cause extension by the blowfly greatly diminish intake of sugar solutions (Evans, in preparation).

#### HUNGER

In a study such as the preceding, it does not appear possible to employ the word "hunger" in a meaningful and useful sense. The term implies a unitary phenomenon; consequently it should refer to a single process which is causally linked to all the overt manifestations of feeding and starvation. Use of the term before there is experimental evidence that such a common path exists is an assumption, conceivably a misleading one. In the present case, the three aspects of behavior that have been studied appear instead to be independent functions. The blowfly may under different conditions be hungry with respect to nutrition, locomotion, or readiness to feed, each independently of

the others. A possible compromise would be to restrict the term to one aspect of the total behavior, most likely to readiness to feed. But this usage becomes repugnant when the animals die of starvation although they will not feed and therefore are not "hungry."

In view of these considerations, the word "hunger" in such cases is at best inutile and is perhaps even prejudicial, except possibly after the fact when the several manifestations have been shown to have a common causation.

#### SUMMARY

Starvation has several behavioral manifestations in the blowfly. At present, taste sensitivity to carbohydrates, food intake, and locomotor activity are recognized, all of which increase during starvation. The mechanisms whereby ingestion accomplishes these changes have been analyzed in physiological terms.

Much evidence indicates that it is the presence or absence of solutions in the foregut, exclusive of the crop, that regulates taste sensitivity to carbohydrates, but the report that transection of the recurrent nerve interferes with threshold regulation could not be confirmed. It is pointed out that a hormonal link in the pathway of threshold regulation has not yet been excluded as a possibility and that such a hypothesis would account for the typical delay of threshold elevation after ingestion.

From the knowledge of the behavioral taste threshold, other aspects of the ingestive act are predictable. An adequate and acceptable stimulus to chemosensory hairs is sufficient to evoke proboscis extension (by definition), spreading of the labellar lobes, and initiation of sucking, all of which continue until adaptation has proceeded to a level that renders the solution effectively tasteless. The "sweetness" of the solution determines the rate of ingestion, as well as affecting adaptation time. After ingestion, the time-course of disadaptation and of threshold elevation determine taste threshold. Thus, the initiation, maintenance, termination, rate, and duration of ingestion are regarded at present as relatively simple neurophysiological functions.

Feeding and starvation apparently act via a different mechanism to affect locomotor activity. If the term "hunger" is employed, one must say that the blowfly may be hungry with respect to nutritional state, to taste threshold or readiness to ingest, and to locomotor activity, each of which is experimentally dissociable from the others.

Some ecological implications of these findings are discussed. A new method of obtaining behavioral taste thresholds is described which gives statistically satisfactory results when as few as twelve flies are employed.

#### ADDENDUM

We and all the earlier references on this subject have apparently been unaware of the pertinent evidence of M. Day (1943. *Biol. Bull.*, 84:127-140) on *Lucilia* and *Sarcophaga* and E. Thomsen (1952. *J. exp. Biol.*, 29:137-172) on *Calliphora*. Both noted in asides to their main points that certain operations on endocrine systems associated with the stomatogastric nervous system

produced bloated flies. Both recognized that the bloating was a consequence of excessive water ingestion and that it developed in only a fraction of the operated flies. Thomsen confirmed Day's observation that removal of the ring gland from flies just after eclosion had this effect. Thomsen obtained similar results upon extirpation of the medial neurosecretory cells of the brain which join the recurrent nerve and end in the endocrine organs of the ring gland. Day also cut the recurrent nerve, apparently without noticing such an effect. While the hyperphagia is not explicable at the present time, these results and our discussion point up several common features: hyperphagia is not an invariable concomitant of any of the several surgical procedures; imbibition of water is responsible for the bloating, at least in part; and the hyperphagia is as closely associated with endocrine systems as with purely nervous pathways.

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# Vegetation Zonation on the Shore of a Small Lake<sup>1</sup>

ADRIENNE MANDOSSIAN

*High School of Commerce, Detroit, Michigan*

and

ROBERT P. McINTOSH

*University of Notre Dame, Notre Dame, Indiana*

The occurrence of more or less well-marked, concentric zones of vegetation parallel to the margins of lakes has been frequently noted and described as zonation (Dansereau 1945, Raup 1935). It is commonly ascribed to the existence of continuous bands of different habitats which parallel the shore line. The distinctiveness of the zones is due to the different physiognomies of the vegetation and presumably the zones are differentiated by their species composition. The zones described may be very wide or, in some cases, narrow bands parallel to the shore. They may be continuous or interrupted by areas of different vegetation, if the environment varies abruptly across the pattern of the zones, resulting in an alternation of different vegetational communities which occupy the same position relative to the shore line (Braun-Blaunquet, 1932). The present work was designed to study quantitatively the composition of zones of vegetation paralleling the shore of a small lake.

## DESCRIPTION OF THE AREA

Duck Lake is a small, dystrophic lake located about one mile northeast of the Kellogg-Gull Lake Biological Station of Michigan State University. (T1S., R9W., Sec. 5, SE ¼) Kalamazoo County, Michigan. It is almost round, quite shallow, and has no outlet or inlet. Much of the shore line has a luxurious zone of *Nuphar advena* which extends well into the body of the lake. The water is alkaline with a pH of 8.0 at the time of the study in July and August of 1959. The water level is controlled by the level of the water table and has fallen during the past ten years exposing a slightly sloping surface (1.5%-2.0%). This study is restricted to the narrow band (7-12 m), on the south shore of the lake, extending from the present water line to a distinct line of shrubs which marks the higher water level. This is comparable to the grève or strand of Dansereau (1945). Local residents said that the line of shrubs marked the shore of the lake ten years ago and it had been at that level for as far back as they could remember. Iron posts for tying up boats and abrupt terminations of paths indicate that this was in fact the old shore line. The study area had been submerged until approximately ten years ago and has been exposed as the water receded. Two distinct bottom

<sup>1</sup> Contribution No. 111 from the Kellogg Gull Lake Biological Station, Hickory Corners, Michigan.

Species	Meter											
	1	2	3	4	5	6	7	8	9	10	11	12
<i>Nuphar advena</i>	20	20	20	15		10	10	30	10			
<i>Potamogeton natans</i>				5								10
<i>Hemicarpha micrantha</i>	95	100	65	50	20	5						
<i>Hydrocotyle umbellata</i>	80	75	70	80	90	30	10	5				5
<i>Carex</i> sp.	15	15	10		10	20	10					
<i>Peltandra virginica</i>		5	5									
<i>Juncus coriaceus</i>			30	15	35	15	5					
<i>Polygonum punctatum</i>			15			5	10	10	10	10		
Gramineae sp.			40	40	20	30	15	20	10			15
<i>Gerardia purpurea</i>					35	30	25	30	25			
<i>Salix</i> sp.				20	10	10						
<i>Cyperus strigosus</i>					20	10		15				
<i>Juncus effusus</i>				30	10	10	50	30	25	10	20	
<i>Juncus tenuis</i>						10	10	20				
<i>Lycopus americanus</i>		10	30	30	40	40	20	20	20	45	25	
<i>Solidago</i> sp.					25	30	35	35	60		45	35
<i>Impatiens pallida</i>							15	5	15	25		
<i>Eupatorium perfoliatum</i>			10	10	40	35	40	35	55	70	70	
<i>Spiraea alba</i>					5							
<i>Carex crus-corvi</i>							10		5	10	25	
<i>Juncus militaris</i>					5				5			
<i>Lactuca canadensis</i>					5			10	15			
<i>Verbena hastata</i>								10			5	
<i>Potentilla anserina</i>										5	5	
<i>Hypericum boreale</i>										5		
<i>Hieracium</i> sp.										10		
<i>Cephalanthus occidentalis</i>											5	15
<i>Aster</i> sp.								10		5		10
<i>Cirsium arvense</i>										15	5	15

TABLE II.—Average frequency per cent in transects on sandy bottom

Species	Meter						
	1	2	3	4	5	6	7
<i>Nuphar advena</i>	3	10	3				
<i>Potamogeton natans</i>	10	7	3				
<i>Hemicarpha micrantha</i>	33	83	87	97	53	43	27
<i>Hydrocotyle umbellata</i>	23	60	73	47	20	53	37
<i>Juncus</i> sp.	10	10	33	13	33		13
<i>Juncus coriaceus</i>		3	50	57	20	17	7
<i>Polygonum punctatum</i>			3	3			
Gramineae sp.		3	13	33	27	13	20
<i>Carex</i> sp.			3	13	27	10	3
<i>Gerardia purpurea</i>			3	40	60	100	80
<i>Salix</i> sp.			3	30	30	17	17
<i>Rorippa palustris</i>			7				
<i>Eleocharis palustris</i>			7	7			
<i>Dulichium arundinaceum</i>				10	7		
<i>Lycopus americanus</i>			7	10	30		3
<i>Carex cryptolepis</i>					13	3	
<i>Impatiens pallida</i>					10	3	10
<i>Eupatorium perfoliatum</i>						3	17
<i>Spiraea alba</i>					10	10	7
<i>Quercus</i> sp.						3	
<i>Juncus tenuis</i>				3		3	
<i>Lycopus uniflorus</i>							13
Fabaceae sp.				7	13		

TABLE III.—Average density on muck bottom of the more common species

Species	Meter											
	1	2	3	4	5	6	7	8	9	10	11	12
<i>Hemicarpha micrantha</i>	78.0	80.0	18.0	10.0	2.5							
<i>Hydrocotyle umbellata</i>	4.0	5.7	9.0	8.7	1.0							
<i>Juncus coriaceus</i>			1.2	1.2	3.7	0.7	0.2					
<i>Gerardia purpurea</i>					1.0	1.0	0.2	1.5	0.5			
<i>Juncus effusus</i>				1.0		0.7	2.5	2.2	1.0		0.5	
<i>Lycopus americanus</i>				1.2	0.2	1.0	0.5		0.5	0.7	0.5	0.2
<i>Solidago</i> sp.				0.2	1.0	1.5	1.2	0.7			1.5	
<i>Eupatorium perfoliatum</i>				0.2	0.2	1.0	1.5	0.5	0.2	1.5	1.7	2.2
Average density of all species.	82.2	86.1	30.2	24.3	9.7	7.5	7.3	6.4	5.0	4.0	5.7	3.2

TABLE IV.—Average density on sandy bottom of the more common species

Species	Meter						
	1	2	3	4	5	6	7
<i>Hemicarpha micrantha</i>	4.8	10.8	11.7	10.3	4.0	3.3	1.0
<i>Hydrocotyle umbellata</i>	1.5	25.7	7.8	1.5	1.0	1.5	0.2
<i>Juncus</i> sp.		0.5	2.7	0.7	0.5	0.8	
<i>Juncus coriaceus</i>		0.3	1.0	2.3	0.5	0.5	
<i>Gerardia purpurea</i>			0.7	2.0	3.2	8.8	6.8
<i>Lycopus americanus</i>					0.3	0.3	0.2
<i>Eupatorium perfoliatum</i>						0.2	0.3
Average density of all species.	6.8	38.2	25.0	19.8	11.0	17.4	9.9

more distant from the water's edge. The first few meters on both sand and muck bottoms are dominated by two small species, *Hemicarpha micrantha* and *Hydrocotyle umbellata* (Tables I-IV). These two constitute over seventy-five per cent of the average density in each of the first three meters on the sand bottom and in the first four meters on the muck although the average density of *Hemicarpha* is much lower on the sand. Beginning with the third and fourth

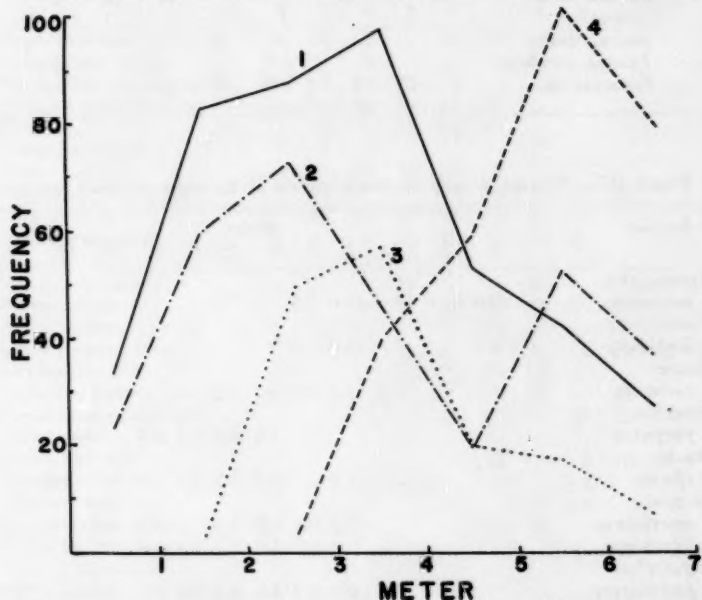


Fig. 1.—Average frequency per cent in each meter of common species on sand bottom. 1. *Hemicarpha micrantha*, 2. *Hydrocotyle umbellata*, 3. *Juncus coriaceus*, 4. *Gerardia purpurea*.

meters larger plants appear which, because of their size, if not their numbers, give the impression of a distinct zonation.

The composition of the vegetation, however, does not exhibit a sharp change at any point along the transect. Rather there is a gradual transition in the composition of successive meters. This is evidenced by the changes in frequency per cent of some of the common species (Figs. 1 and 2). Similar changes are exhibited if average density is used instead of frequency.

It is not surprising to note that the average density, especially in the muck transects, diminishes in the segments of the transect farther from the shore line (Table III). This is due simply to the larger size of the individual plants relative to the sample size (1 dm<sup>2</sup>). The first two meters of both sand and muck bottoms are very similar in composition, *Hemicarpha* and *Hydrocotyle* comprising over ninety per cent of the relative density in both cases. Beyond the second meter the proportion of these two species drops off and does so more rapidly in the muck transects than in the sand transects. This is also true of the average density and average frequency.

The change in composition is also illustrated by comparing each meter with the others by means of the "Index of Similarity" (Bray

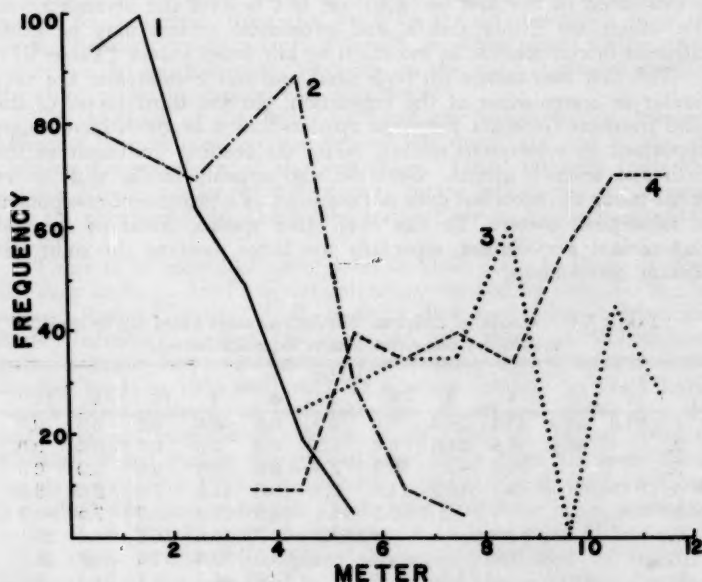


Fig. 2.—Average frequency per cent in each meter of common species on muck bottom. 1. *Hemicarpha micrantha*, 2. *Hydrocotyle umbellata*, 3. *Solidago* sp., 4. *Eupatorium perfoliatum*.

[illegible]

## DISCUSSION

The exposure of two very different types of substrate, sand and muck, as a result of the lowered water level of the lake affords an opportunity to examine and compare the composition and distribution of the vegetation occupying the newly exposed areas. The first four meters in either case are dominated by the same species, *Hydrocotyle umbellata* and *Hemicarpha micrantha*. The water level and perhaps physical or chemical characteristics of the water are apparently the primary factors influencing the vegetation in these segments of the transects. This is suggested by the gradual diminution in the importance of the two major dominants in each successive meter away from the water's edge. In some species, especially *Gerardia purpurea*, the individual plants nearest the water's edge were small and spindly and increased in size away from the water's edge.

Beyond the fourth meter the vegetation on sand and muck become increasingly dissimilar so that by the last comparable meter, the seventh, there is little or no similarity between the vegetation on the two substrates. Here the difference in the substrate, especially the ability of the muck to hold and supply water more effectively than the sand, becomes of primary importance. This is made evident by the persistence of hydrophytes such as *Nuphar advena* and *Potamogeton natans* much farther from the water's edge on the muck than on sand. *Nuphar* persists as large although prostrate plants to the ninth meter on the muck bottom, whereas, on the sand it persists only to the third meter as depauperate specimens.

The vagaries of the Index of Similarity values in the transect segments beyond the fourth meter on the muck are due to the increasing heterogeneity of the vegetation. Once distance from the water's edge is no longer the primary factor influencing the vegetation the proximate segments in the transect are no longer particularly similar.

There is no record of water level at Duck Lake to show whether the drop in water level was continuous or marked by irregular fluctuations. Records of the W. K. Kellogg Bird Sanctuary of Michigan State University, located less than one mile away on Wintergreen Lake, indicate that levels at Wintergreen Lake have dropped, reaching low levels in 1958 and 1959. If it reacts similarly to Duck Lake, which seems probable as both lakes are runoff and spring fed, the drop was not continuous. Water levels show an annual cycle of fluctuation and though the general trend since 1949 has been down, an abrupt drop in 1953 is followed by a slight rise in 1954-1955 and a gradual, continuous drop to 1959. The past three years, according to Dr. R. D. Van Deusen, the Director, have been years of low water.

A study of shore line plant succession controlled by irregular fluctuations of the lake level by Graham and Henry (1933) describes the resulting vegetation as forming discrete zones as seral units. Galiano (1957) also describes well defined associations (*sensu* Braun-Blanquet) related to annual changes in water level.

The results of the present study indicate a gradual change in composition along the transects. The apparent zonation close to the shore line is due to a physiognomic distinction rather than a compositional one. The specific composition of the vegetation and the changes noted are not necessarily typical of lakes in this region. At least little comparative data of a quantitative nature is available. In this instance the apparent zones are not divisible into well-defined communities or zonal bands by any but arbitrary criteria.

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# Structure and Functions of the Thyroid Gland in Reptiles<sup>1</sup>

W. GARDNER LYNN

Department of Biology, The Catholic University of America,  
Washington, D. C.

Reference to recent general reviews concerning thyroid morphology and physiology reveals a paucity of information for Reptilia as compared with any other vertebrate class (Eggert, 1938; Goldsmith, 1949; Fleischmann, 1951; Lynn and Wachowski, 1951; Gorbman, 1955; Kollros, 1959). This paper gives an account of the present state of knowledge of the reptilian thyroid in the hope of stimulating further researches in this field.

## HISTORICAL

Although several early anatomists noted the thyroid gland in a few reptiles, Simon (1844) seems to have been the first to clearly distinguish thyroid from thymus in lower vertebrates and to attempt a comparative account of its morphology. Leydig (1853) made an early study of both gross and finer structure of the thyroids of *Testudo graeca* and *Coluber natrix*. The first embryological investigation of the gland in a reptile is that of de Meuron (1886) for *Lacerta agilis*. Experimental approach to study of the functions of the reptilian thyroid began with the work of Christiani (1894a,b, 1895a,b,c, 1900, 1903) who devised methods for thyroidectomy and thyroid transplantation in lizards, snakes, and turtles.

## GROSS MORPHOLOGY

In turtles and in snakes the thyroid is an unpaired gland, spherical, ellipsoidal, or ovoid in shape, just anterior to the heart. In Crocodilia it consists of two well-defined lobes lying on either side of the trachea with a narrow connecting isthmus. In *Sphenodon* it is a single, narrow body, transversely elongate. Lizards show a wide variety of thyroid forms with unpaired, bilobed, and completely paired glands found even in different members of the same family.

Detailed descriptions of the anatomical relations of the thyroid are available for a number of lizards and for *Sphenodon*. For other reptiles published information is scanty.

Study of the lizard thyroid begins with the work of Simon (1844) who pointed out the wide diversity of thyroid form in the Lacertilia as exemplified in representatives of the families Lacertidae, Iguanidae, Gekkonidae, Chameleontidae, Scincidae, and Amphisbaenidae. The

<sup>1</sup> This study was supported by United States Public Health Service Grant No. A-2921.

bilobed thyroid of *Uromastix* was described by Calori (1862) and that of *Phyllodactylus* by Wiedersheim (1876). Van Bemmelen (1887) gave a brief account of the vascular supply to the gland in *Platy-dactylus*, *Anguis*, and *Lacerta* chiefly emphasizing the presence of two pairs of thyroid arteries. Thyroid morphology in several African lizards was discussed by Viguier (1909a,b, 1911a). The arterial supply was given for *Uromastix* by Bhatia (1929) and for *Hemidactylus* by Bhatia and Dayal (1933). Bourne (1935) considered the thyroid of *Egernia kingii* as unique in being a narrow, ribbon-like structure lying transversely across the trachea but this condition is found in a number of other lizards (Lynn and Walsh, 1957).

The most complete account of the anatomical relations of the thyroid in a lizard is that of Adams (1939) for *Lacerta*. In this animal the gland lies dorsal to the muscles constrictor colli, episterno-hyoideus superficialis and profundus as a broad structure widest at the center and tapering at the ends. It is ventral to the trachea and just anterior to the divergence of the carotid arches. The arterial supply is by a pair of superior thyroid arteries arising from the external carotids and a pair of inferior thyroids from the laryngo-tracheal branch of the pulmonary artery. Paired thyroid veins enter the vena trachealis (external jugular of Bourne) which, in *Lacerta*, is present on the right side only. Innervation is from the inferior laryngeal nerves. Miller (1955) described a quite similar vascular supply in *Xantusia*.

A recent survey of thyroid morphology in representatives of 23 families of lizards (Lynn and Walsh, 1957; Lynn and Komorowski, 1957) emphasizes the multiplicity of forms assumed by the gland in this group and the wide divergence from the usual condition which may be found in certain specialized families like the Amphisbaenidae where the thyroid may be extremely long and attenuated and situated far anterior to the heart.

The lizard thyroid is usually contained in a large lymphatic space and is often also enveloped in adipose tissue (Pischinger, 1937). In *Gymnodactylus* the gland is reported to be fused with a thymus-like tissue complex (Eggert, 1934b).

Although the turtle is widely used as a laboratory animal the only full account of thyroid morphology is that of Naccarati (1922) for *Emys europaea* and *Testudo graeca*. In these the gland is spheroidal, located a little to the right of the midline in the cavity of the arch of the innominate trunk. Volume and weight of the thyroid show a high degree of individual variation. In *Emys* it lies at the level of the divergence of the bronchi, in *Testudo* it is posterior to this level. Paired superior and inferior thyroid arteries arise from innominate trunks and carotid arteries respectively. The paired thyroid veins unite with the accessory pectoral veins and enter the subclavians. A rich lymphatic drainage is present. Innervation is from the cervical sympathetics and the laryngeal branches of the vagi.

Published accounts of ophidian thyroid morphology are limited

to brief descriptions for two subspecies of the water-snake, *Natrix sipedon* (Thompson, 1910; Bragdon, 1953) and some incidental observations on *Zamenis* and *Coleopeltis* (Francescon, 1929).

No paper dealing with the gross anatomy of the crocodilian thyroid has come to hand.

*Sphenodon*, the sole living representative of the Rhynchocephalia, has naturally attracted special interest. Its thyroid was described by van Bemmelen (1887) who noted the presence of two pairs of thyroid arteries just as in lizards. O'Donoghue (1920), in a detailed study of the vascular system described the superior thyroid arteries as branches of the external carotids and the inferior thyroids as branches from the pulmonary arch. The thyroid veins enter the precaval by way of the brachials. Adams (1939) noted that the anatomical relations of the thyroid in *Sphenodon* are similar to those in *Lacerta*.

Gross pathological enlargement of the reptilian thyroid seems rare. Only two cases have come to notice. Pick and Poll (1903) described a large adenomatous goiter in a pleurodiran turtle (*Platemys*) and Muller (1926) recorded a parenchymatous and cystic colloid goiter in the lizard *Zonurus*. Both these animals had been kept in captivity for some years.

#### EMBRYOLOGY

The origin and early development of the reptilian thyroid shows no unusual features. The anlage of the gland arises as an evagination of the pharyngeal floor at the level of the first pair of pouches. Paired lateral anlagen do not seem to be involved in any reptile. After separation from the pharynx the cells of the thyroid rudiment become arranged into cords or clumps. As posterior migration occurs the gland becomes encapsulated and the cell cords break up into organized follicles. Various aspects of these phases of development have been described for lizards (*Lacerta*: de Meuron, 1886; Maurer, 1898, 1899; Peter, 1901; Eggert 1934a; *Anguis*: Prenant, 1896; *Tarentola*: Viguier, 1909a; *Seps*: Dorello, 1909a, b; *Sphaerodactylus*: Walker, 1951; Cheverie, 1959), turtles (*Chelonia*: van Bemmelen, 1893; *Chrysemys*: von Alten, 1914; Shaner, 1921; *Chelydra*: Dimond, 1952), crocodilians (*Alligator*: Reese, 1910; Hammar, 1937; *Crocodilus* and *Kaiman*: Hammar, 1937) and one snake (*Thamnophis*: Harrison and Denning, 1929). The embryology of the thyroid of *Sphenodon* has not been described.

The time of appearance of organized follicles and of colloid within the follicles is of interest since these features may be taken as indications of the onset of secretory activity. Only a few of the papers cited give precise information on these points. Maurer (1899) found organized follicles beginning to form in embryos of *Lacerta agilis* 21 days after the eggs were laid but colloid was first seen at 31 days (the next stage studied). Eggert's (1934a) much more detailed study for this species and for *L. vivipara* revealed somewhat earlier appearance of these features: follicles well defined at 20 days

(Peter's Stage 32); intrafollicular colloid at Stage 33. Recent work of Cheverie (1959) on *Sphaerodactylus* agrees closely with Eggert's findings. In the turtle, *Chelydra*, (Dimond, 1952) follicles first appear in the 20-day embryo but stainable colloid is not present until the 23rd day.

#### HISTOLOGY AND CYTOLOGY

Detailed histological consideration of the reptilian thyroid began with Galeotti's (1896) account of the changes in the follicular epithelium in turtles treated with certain toxins. Later Viguiet (1909a, b, 1911a) gave brief descriptions of normal thyroid histology in several lizards and Naccarati (1922) provided rather full accounts for *Emys* and *Testudo*. Barchiesi (1928) discussed the effects of prolonged starvation upon the turtle thyroid and pointed out, what is now well recognized, the enormous variability in thyroid histology in normal turtles. Bussi (1929) described the reticular network around the thyroid follicles in several reptiles as well as in birds and amphibians. The general histology of the snake thyroid has been described by Hellbaum (1936).

Beginning with the work of Weigmann (1932) there has been considerable interest in seasonal changes in the activity of the reptilian thyroid and this has resulted in the publication of several important histological studies. Weigmann found significant seasonal changes in epithelial height in the thyroid of *Lacerta vivipara* which indicated a much greater functional activity in summer than in winter. Eggert (1935a) carried out a detailed study over a period of several successive seasons for three different species of *Lacerta* and for animals of various ages. He found that the thyroid exhibits signs of maximal activity during June and July. At this time all follicles contain thin, freshly formed colloid with many peripheral chromophobe droplets. The epithelium is high and many cells exhibit mitotic figures. Epithelial height and mitotic rate gradually decrease during late August and September and there is an increase in stored colloid. The gland is most inactive during the winter months when the lizards are in deep hibernation. In young specimens activity begins anew in February and the thick stored colloid is gradually released and replaced by thin newly produced secretion. By April the gland is rather active with only a few peripheral follicles still containing stored colloid. Experiments on the effects of high and low temperature led to the conclusion that the seasonal changes are largely dependent upon environmental temperature (Eggert, 1935b). In addition to the seasonal changes the thyroid also shows brief periods of decreased activity in relation to the growth of the horny layer of the skin preceding ecdysis. Once shedding has occurred the thyroid returns to its normal appearance within 48 to 72 hours. Eggert found no evidence of changes in histology correlated with the breeding season in *Lacerta*.

Wilhoft's (1958) findings for *Sceloporus occidentalis* are in agreement with those of Eggert. Height of the thyroid epithelium is low-

est during the winter (December to February) and highest in summer (June and July). The epithelial height increases gradually during the mating period (April to June). In females the histological appearance of the thyroid indicates a rapid decrease in activity shortly after egg laying. In males there is a more gradual decrease beginning somewhat later. Juveniles show an increase in activity in the spring which reaches a maximum during June and July. Wilhoft also demonstrated that prolonged exposure to temperatures which are optimal for normal activity (34-35°C) causes death in some animals, a greater frequency of molting in some, and a rise in heart rate and in thyroid epithelial height in all.

In non-hibernating lizards (*Anolis carolinensis* from Louisiana) thyroid histology indicates high secretory activity even during the coldest months and the lowest epithelial heights are found during spring and early summer (Evans and Hegre, 1938). In this species an increase in epithelial height occurs in females during ovulation. The viviparous lizard *Xantusia vigilis*, another non-hibernating form, also shows indication of high secretory activity in the winter, December through March, but a further increase in activity during April, May and early June when gametogenesis and mating occur (Miller, 1955). In females the thyroid continues to present an appearance of high activity during early gestation but becomes relatively inactive before parturition. The epithelial height reaches its lowest level during late fall (August to December).

Study of the thyroids of turtles (*Chrysemys*) from Montana showed a mid-winter period of inactivity comparable to that found in hibernating lizards (Evans and Hegre, 1940).

Eggert (1935a) also reported age changes in the histology of the lizard thyroid. These are primarily associated with a gradual invasion of the gland by lymphocytes which may form nodules or may spread diffusely through the tissue. Isolated follicles may undergo involution and the spaces resulting from their degeneration are then filled in with fat. Desquamation of the follicular epithelium was also observed in a few specimens. This was not correlated with any particular physiological state or with any phase of colloid release. The shed epithelial cells gradually degenerate and are taken up by lymphocytes.

#### IODINE CONTENT OF THE THYROID

The chemistry of the thyroid secretion is similar in all vertebrates studied. In snakes and fresh-water turtles the iodine content of the thyroid in relation to total body weight is quite comparable to that in other vertebrates (Nosaka, 1926) but the thyroxin content of the gland in sea turtles and alligators is reported to be exceptionally high (Baumann, Metzger and Marine, 1942). Feeding of dried thyroid material from lizards, alligators, or turtles is highly effective in inducing precocious metamorphosis of tadpoles (Drzewicki, 1931, Baumann *et al.*, 1942) and turtle and alligator thyroid effectively raises the basal metabolic rate in rabbits (Swingle and Martin, 1926).

Uptake of radioiodine by the turtle thyroid is subject to great seasonal and individual variation but is within the limits of that found for other animals (Bileau, 1956).

#### THYROID-PITUITARY RELATIONS

##### EFFECTS OF THYROIDECTOMY, HYPOPHYSECTOMY OR TSH ADMINISTRATION

It was pointed out quite early (Viguiet, 1911c) that the pituitary glands of thyroidectomized lizards (*Uromastix*) increases in size and show vacuolization of the basophil cells. Viguiet suggested that the hyperactivity of the pituitary partially compensates for the lack of thyroid secretion. Despite the great interest in thyroid-pituitary relations in vertebrates since that time, only one other paper dealing with the effects of thyroidectomy upon pituitary histology in a reptile has appeared. Siler (1936) found an increase in the number and size of vacuoles in the basophils of the pars anterior of the pituitary after thyroidectomy in the garter snake (*Thamnophis*). There was also an increase in the number of basophils by enlargement and granulation of some chromophobes. The vacuolated basophils ultimately underwent degeneration so that the final result was an actual reduction in pituitary basophils.

Combescot (1955) described characteristic changes in basophils in the turtle (*Emys*) correlated with stages of the reproductive cycle and related these to concomitant changes in thyroid histology. Seasonal changes in pituitary cytology occur also in the garter snake (Hartmann, 1944).

More direct evidence of pituitary control of thyroid function may be derived from studies of the effects of hypophysectomy or of the administration of pituitary extracts. Eggert (1935b) demonstrated the effectiveness of thyrotrophic hormone (TSH) in stimulating thyroid activity in *Lacerta*. Although there is great individual variation in the degree of response, animals given TSH during the summer show a marked increase in the height of the thyroid epithelium, rapid discharge of intrafollicular colloid, and appearance of many intracellular colloid droplets. There is also an increase in mitotic rate which leads to formation of a multi-layered epithelium and ultimately to desquamation of epithelial cells. In hibernating animals however, activation of the thyroid by TSH was not demonstrable. Administration of thyroxine to summer specimens results in rapid reduction in thyroid activity but winter specimens show no response to the treatment. As Eggert points out, this agrees with the hypothesis that a high level of thyroid secretion in the blood serves to depress the pituitary's TSH production. The lizard *Sceloporus* was used by Gorbman (1946) as a test animal for detecting qualitative variations in activity of thyrotrophic hormone preparations, and Mason (1938) suggested the use of the snake *Tropidonotus* for the same purpose.

In snakes (*Thamnophis*) hypophysectomy causes a progressive decrease in the height of the thyroid epithelium which may be cor-

rected by hypophyseal implants (Schaefer, 1933) or by pituitary extract injections (Hellbaum, 1936).

In turtles (*Chrysemys*) a series of 36 daily injections of whole gland pituitary extract causes an increase in height of the thyroid epithelium and a decrease in follicle size which persists as long as 136 days after the first injection (Evans and Hegre, 1940).

#### EFFECTS OF GOITROGENIC DRUGS

Drugs which interfere with production of the thyroid hormone may be used as a means of effecting "chemical thyroidectomy" and thus furnish an additional method for study of the pituitary response to thyroid deficiency. The earliest use of this technique in reptiles seems to have been by Greenberg (1948) who reported increase in epithelial height and discharge of colloid in the thyroids of young turtles (*Pseudemys*) treated with thiourea. Similar responses were obtained by Pastore (1950) in adult *Clemmys* and *Graptemys* and by Adams and Craig (1950b) in *Chrysemys*. In both these latter studies a great individual variability in degree of responsiveness was noted. Dimond (1954) investigated the effects of thiourea on the embryonic thyroid in *Chelydra* and found that hypertrophy, hyperemia, and colloid discharge is produced in the thyroids of all treated embryos whether the drug is administered early or late in the incubation period.

Lizards of the genus *Anolis* show marked thyroid response to antithyroid agents (Adams and Craig, 1949, 1951; Ratzersdorfer, Gordon, and Charipper, 1949) but *Lacerta* is reported to be almost completely unreactive (Adams and Craig 1950a). In *Anolis* injections of 1.0 per cent thiourea are most effective (Ratzersdorfer *et al.*, 1949) and higher concentrations (2.0%) have toxic effects that partially mask the goitrogenic reaction.

The accepted interpretation of the action of goitrogenic drugs is that they interfere with synthesis of thyroid hormone. The resulting decline in the blood level of thyroid hormone stimulates the pituitary to increase its output of TSH and this is responsible for the histological changes in the thyroid itself. The fact that these drugs do indeed affect hormone production by the thyroid has been demonstrated for many vertebrates by measurement of the thyroid's ability to concentrate radioiodine. Only one such investigation has been made for a reptile. This is the study of Bileau (1956) for *Chrysemys*. Her results confirm previous reports of great variability and relatively low sensitivity of response of the turtle thyroid to goitrogens.

#### THYROID RELATIONS WITH OTHER ENDOCRINE ORGANS

Several early workers reported that thyroidectomy in lizards causes definite changes in other endocrine organs of the pharyngeal region. Viguier (1911b) described cytological changes in the parathyroids of *Uromastix* after thyroid removal and Drzewicki (1927) found similar effects in *Lacerta*. Drzewicki (1929) and Sembrat and Drzewicki (1936) reported cystic changes in the thymus and hyper-

trophy of the ultimobranchial (postbranchial) bodies of thyroidectomized lizards. The effects on the ultimobranchial bodies were further studied by Eggert (1936b, 1937, 1938b) who ascribed them to direct action of the increased TSH production following thyroid extirpation. He found that the changes can be produced in intact animals by TSH administration alone.

Relations between thyroid activity and gonadal function seem to be well established for some lizards. Mellish and Meyer (1937) found that mature females of *Phrynosoma* show marked atrophy of the ovaries after thyroxin injection. Moreover the thyroids of lizards (*Anolis*) injected with theelin have smaller follicles and higher epithelial cells than do those of controls (Evans and Hegre, 1938). Epithelial height is also increased during normal ovulation. Similar findings have been reported for the Japanese lizard *Takydromus* (Hatta, 1944). The most recent and most complete studies concerning the relation between gonadal activity and the thyroid-pituitary complex are those of Miller (1948, 1955) for *Xantusia*.

#### THE THYROID IN GROWTH AND DIFFERENTIATION

There is little convincing evidence as to whether the thyroid influences growth rate in reptiles. Drzewicki (1929) reported inhibition of growth following thyroidectomy in young *Lacerta* and Giusti (1931), on the basis of observations on a single thyroidectomized turtle (*Clemmys*), noted a similar retardation. On the other hand Krockert (1941), also on the basis of a single experimental animal, found that feeding pig thyroid gland to a young python resulted in significant growth inhibition as compared with a control. Wilhoft (1958) suggested that histological evidence of increased secretory activity in the thyroids of young *Sceloporus* is related to growth as well as to the time of exposure to optimal temperatures.

The relation of thyroid function to growth and differentiation during embryonic stages has been studied by Dimond (1954) for the turtle *Chelydra*. Developing eggs were treated with thiourea solutions either by direct injection through the shell or by raising the eggs on cotton soaked in these solutions so as to permit gradual absorption. With optimal concentrations and periods of treatment definite inhibition of thyroid activity was produced as indicated by the characteristic histological response to the goitrogen. When such inhibition was effected the development of the embryo was clearly modified. Growth rate was decreased, abnormalities of the carapace appeared, hatching was greatly delayed, and retraction of the yolk sac, which normally occurs at hatching, failed to take place. Thyroidectomy of pregnant females of *Lacerta* some six to eight weeks before the time for egg laying may result in the death of the embryos or, in cases where the eggs are laid normally, in inability of the young to hatch (Eggert, 1933). It seems clear that in these reptiles, as in birds, the thyroid is important in certain aspects of late embryonic development and particularly in relation to the hatching process.

## THE THYROID AND METABOLISM

Although the role of the thyroid hormone in the control of metabolic rate in warm-blooded vertebrates is well known, unequivocal evidence for a similar function in poikilotherms is still lacking. The few papers relating to this problem in reptiles are nearly all concerned with lizards.

Weigmann's (1932) account of seasonal changes in thyroid histology in *Lacerta* was accompanied by a study of seasonal differences in metabolic rate. Measurements of  $\text{CO}_2$  production at two different temperatures, 15° and 29° C., were made on freshly collected specimens for each month in the year. The metabolic activity, at either temperature, was found to be higher in summer than in winter. Moreover the curve, at either temperature, shows a marked rise in the spring after hibernation. Weigmann considered the spring rise as related to reproductive activity and not directly to the thyroid, but the decrease in metabolic rate in winter was regarded as at least partly the result of decreased thyroid activity.

Eggert (1933) interpreted the effects of the thyroid on shedding of the skin in *Lacerta* as being brought about through control of total metabolism. He maintained that the gas exchange of the animal is markedly lowered as a result of a low level of thyroid activity just before shedding. However this hypothesis was not tested by any measurements of metabolic rate. Eggert (1936a) also concluded that the ultimate death of thyroidectomized lizards is ascribable to a decrease in a number of metabolic processes which causes gradual weakening of the animal.

Experiments involving direct measurement of oxygen consumption in lizards indicate that the thyroid does not affect oxidative metabolism. Maher and Levedahl (1957), using a modified Warburg-Barcroft system, measured oxygen consumption in normal, thyroidectomized, and thyroxin-treated animals at different temperatures and at different seasons. They found no significant differences between controls and experimentals in either group.

Lizards (*Sceloporus*) kept for some weeks at widely differing environmental temperatures show differences in thyroid histology which indicate a great increase in thyroid activity at high temperature (35° C) (Wilhoft, 1958). Whether this is simply one aspect of a general rise in physiological activity or is itself partly responsible for an increase in metabolic rate remains to be ascertained.

Krockert (1941) ascribed a loss of weight in a thyroxin-treated *Python* to increased metabolic rate. However, Drexler and von Issekutz (1935) found no change in oxygen consumption in turtles given thyroxin or thyrotrophic hormone and isolated turtle heart also fails to respond to thyroxin (Harvey and MacRae, 1931). On the other hand, blood drawn from alligators given previous treatment with thyroxin shows a higher oxygen consumption than does the blood of controls (Hopping, 1931; Scott, 1935). The acid-base balance of the blood is also affected by the thyroxin treatment. Destruction of thyroxin

in the blood of the alligator is apparently very slow; the increase in oxygen consumption is still demonstrable six months after thyroxin injection.

#### THE THYROID AND ECDYSIS

In the Squamata, lizards and snakes, which undergo periodic ecdysis or shedding of the outer layer of the skin, a relation of thyroid function to this process is strongly indicated. Curiously enough, however, the thyroid hormone seems to stimulate ecdysis in one group and inhibit it in the other.

Drzewicki (1926) was the first to report that thyroidectomy in lizards (*Lacerta*) results in a cessation of molting. In subsequent papers (1927, 1929) he described in detail the histological changes in the skin following thyroid removal. He reported that the horny layer of the skin is formed continuously in thyroidless animals and the periodic formation of a border sheet (*stratum terminativum*) fails to occur. For this reason the outer cornified layers do not separate off but pile up to form a thick, rough, wrinkled covering over the whole body. This even involves the eyes, the conjunctival epithelium becoming horny and many-layered so that the animals are usually blind within 3 to 5 months.

Drzewicki's findings were not confirmed by Noble and Bradley (1933) for the lizard *Hemidactylus*. Neither hypophysectomy nor thyroidectomy causes cessation of ecdysis in this animal although either operation does result in a lengthening of the period between molts. Thyroxin injections cause a return of the molt to its normal periodicity. However, thyroxin administration to unoperated specimens does not decrease the periods between molts. Noble and Bradley noted that Drzewicki had used only a small series of lizards and suggested that his results might have been due to poor health in his animals.

However, Eggert's (1933, 1936a) exhaustive investigations for three different species of *Lacerta* fully confirmed Drzewicki's conclusions for this genus and further demonstrated that definite changes in thyroid histology are correlated with specific phases of epidermal differentiation and ecdysis. Active formation of new epidermis occurs during about the last third of the interval between molts. Within a few days after the beginning of this new growth the thyroid begins a decrease in epithelial height and shows other indications of declining secretory activity. Cornification of the old uncornified epidermis as well as of the newly formed sheets of cells occurs during this time. Colloid storage is at its maximum in the thyroid during the period when the loose horny sheet is differentiating. The process of molting, which takes only a few hours, then follows. With the beginning of molting the thyroid shows increased production of new colloid and release of stored colloid, epithelial height increases and chromophobe droplets become numerous. By the end of molting most follicles are in the active phase and all follicles appear active within 3-4 days after ecdysis. Thyroidectomy causes complete cessation of shedding

but homoplastic implantation of thyroid tissue into the back muscles of thyroidectomized animals is followed by at least one or two successful molts.

Sembrat and Drzewicki (1935, 1936) in further experiments with *Lacerta* showed that in thyroidectomized animals which have ceased to shed, a new molt can be induced by implantation of thyroid material from the shark *Scylliorhinus*. They point out that the shark itself never undergoes a molting process. The ability of its thyroid secretion to induce ecdyses in lizards may be considered to support Eggert's conclusion that the effect is due to a general influence on metabolism rather than to any specific principle related to molting.

Adams and Craig (1950a) also confirmed the fact that thyroidectomy results in cessation of molts in *Lacerta*. They found, however, that administration of goitrogens (thiourea, thiouracil) did not affect molting. It seems clear that this was due to insufficient dosage of the goitrogens for the thyroids of these treated animals also failed to show any significant effects. In another lizard (*Anolis*) Adams and Craig (1949) did obtain thyroid hyperplasia after goitrogen administration but unfortunately did not have sufficient data to make conclusions on molting. Ratzersdorfer, Gordon, and Charipper (1949) also found that thiourea injections induce thyroid hyperplasia in *Anolis* and that this reaction can be prevented by simultaneous administration of thyroxine. In their experiments the thiourea treatment did not cause cessation of molting or even affect the interval between molts although they did note an increase in the time required for the actual molting process.

It seems quite clear that the process of ecdysis is strongly influenced by thyroid activity in lizards. However, in view of the differences reported for the three genera which have been studied, more extensive investigations for still other genera are highly desirable.

Present evidence indicates that the thyroid influence on molting in snakes is the opposite of that in lizards. Schaefer (1933) reported that either hypophysectomy or thyroidectomy causes an increase in molting activity in garter snakes. Operated animals were found to shed 5 or 6 times during the period when similarly fed controls shed only once. Feeding of desiccated thyroid tissue to hypophysectomized or thyroidectomized specimens prevented shedding. Schaefer maintained that the effect of the thyroid on ecdysis cannot be explained merely on the basis of a lowering of the metabolic rate, for animals kept at hibernating temperatures for several months did not shed at all.

Krockert's (1941) experiment on thyroid-feeding in *Python* is in agreement with Schaefer's findings. His thyroid-treated animal shed only 4 times in 16 months whereas control and pineal-fed specimens molted 8 times during this period. The thyroid-fed snake returned to a normal shedding rate about year after cessation of treatment.

The experiments of Halberkann (1953, 1954a, b) demonstrated

these same relations for *Natrix*. Thyroxin or TSH administration inhibits shedding while treatment with a thyroid-inhibiting drug (methylthiouracil) causes an increase in the number of molts.

#### MISCELLANEOUS EFFECTS OF THYROID HORMONE

Eggert (1933, 1936a) has shown that complete thyroidectomy in *Lacerta* results in ultimate death after periods of 3 to 8 months. The main cause of death is an anemia attributable to a marked decrease in blood-forming activity in bone marrow. There is also a gradual decrease in activity and appetite with a mobilization of fat reserves. The animals finally refuse to eat and die in a cachetic condition. All of these effects can be alleviated or prevented by homoplastic thyroid implantation or by thyroxin administration. In *Hemidactylus*, on the other hand, Noble and Bradley (1933) found that thyroidectomized animals show no differences in behavior and no increase in death rate as compared with controls. The survival time of their specimens is not given, however.

A relation between the thyroid and blood formation has been reported by Charipper and Davis (1932) for the turtle *Pseudemys*. They found that thyroxin administration results in increase in the leucocyte count by stimulating granulocytopoietic centers so as to cause an increase in the number of young eosinophils. This they considered analogous to a left-hand deflection of the polymorphonuclear count previously reported for amphibians, birds, and mammals.

Thyroid effects on behavior are mostly concerned with hibernation and breeding activity and these have already been considered. Evans and Clapp (1940) noted that territorial behavior, the urge to defend a specific home territory, and general pugnacity are increased in both sexes of *Anolis* by injection of thyroxin or TSH. Krockert (1941), on the basis of thyroid feeding of a single young python, reported a great increase in irritability as compared with an untreated and a pineal-fed litter-mate.

#### SUMMARY

The reptilian thyroid is always a well-defined encapsulated gland. In turtles, snakes, and *Sphenodon* it is unpaired; in Crocodilia it is markedly bilobed. Among lizards there is wide diversity in thyroid morphology and position. Embryonic origin and early development of the gland show no unusual features.

The fundamental histology of the reptilian thyroid agrees with that found in other amniotes. Seasonal changes in histology both in relation to temperature and breeding season are of particular interest. Studies of these matters are available for several lizards but further investigations are much needed for both hibernating and non-hibernating lizards and especially for snakes, turtles, and crocodilians. In lizards it has been demonstrated that the thyroid shows well-defined histological changes in relation to differentiation and shedding of

the horny layer of the skin. In view of the fact that thyroid function also plays a role in ecdysis in snakes, similar studies should be carried out on representatives of this group.

Pituitary control of thyroid activity by means of thyrotrophic hormone is well demonstrated for reptiles as for other vertebrates. Response to various antithyroid agents seems to differ markedly in different reptiles, however, and this subject deserves further study. The reported effects of thyroidectomy upon other endocrine organs such as parathyroid, thymus, ultimobranchial body, and gonad also require more extensive investigation.

There is some evidence that the growth rate of reptiles, both at embryonic and post-embryonic stages, is affected by the thyroid hormone. More critical studies on a wider variety of forms will be necessary before the nature and extent of this effect can be defined. The importance of the thyroid in certain aspects of late embryonic development and hatching has been demonstrated for one turtle and one lizard. Again the need for more comprehensive investigations is obvious.

As is the case for other cold-blooded vertebrates, the significance of the thyroid in metabolism of reptiles is far from clear. Most authors who have assumed that the reptilian thyroid affects metabolic rate have based their conclusions on circumstantial evidence. Only experiments involving direct measurement of appropriate metabolic processes can solve this problem.

The fact that the thyroid plays an important role in ecdysis in *Lacerta* is well established. However, the representatives of two other genera of lizards which have been studied show rather marked differences in response. Moreover, the effect of the thyroid on molting in snakes seems to be just the opposite of that in lizards. Further experiments on this matter are much needed in both groups.

The use of radioiodine as a tool in study of thyroid function is a promising technique which remains almost entirely unexploited for reptiles. Investigations concerning iodine uptake and turnover at different seasons, under different environmental conditions, at different phases of the reproductive and molting cycles, and under various treatments would go far to elucidate some of the unsolved problems mentioned above.

The reptiles occupy a unique position among vertebrates as the only cold-blooded amniotes. The number of types of reptiles readily available as experimental animals is gradually increasing. Recent advances in histological techniques and experimental methods have largely superseded many of those used in the earlier investigations reviewed above. General interest in reptilian physiology seems to be on the rise. It is to be expected that within a short time these factors will combine to provide a considerable increase in our knowledge of the reptilian thyroid.

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# Postmetamorphic Growth in Anurans<sup>1</sup>

FREDERICK B. TURNER

Wayne State University, Detroit, Michigan

Knowledge of the rate of growth and time of sexual maturity is necessary in analyzing the age structure, survival rate and reproductive potential of anuran populations. Growth rates of transformed anurans have been determined in three ways, depending on measurements of (1) preserved materials, (2) captive individuals, and (3) individuals, either marked, or in large samples taken from the same natural population at different times during the same growing season.

Except for the first two or three-year classes, the identification of age groups is impossible in samples from different, or even the same, populations. Nevertheless, Wright (1932) presented growth rates of 19 anuran species from Georgia based primarily on size-frequency distributions. Subsequent analyses of anuran growth rates in Florida (Pearson, 1955; Hamilton, 1955) have confirmed some of Wright's conclusions. On the other hand, Wright's (1920, 1932) estimates of growth in *Rana catesbeiana*, based on northern material, do not agree with findings of later workers (Raney and Ingram, 1941; Ryan, 1953).

Growth rates of captive individuals, as reported by Flower (1925, 1936), Cowan (1941), and Wilson (1950), are of questionable validity as estimates of growth rates of individuals under natural conditions.

There are few studies of growth under natural conditions. Force (1933) and Bannikov (1950) depended on modal size differences in mass samples collected at the same locality at different times. This technique reveals the average growth rate but tends to obscure the magnitude of individual variation. Furthermore, this method is most effective when the growth rate is fast enough to give a recognizable modal difference within a period of a few weeks. The time element may be critical—unless the entire population is restricted to a small area, movements or ecological shifts may modify the age structure of the second sample (with reference to the first) and invalidate the whole procedure.

Other studies have been based on the growth of marked *individuals* in a natural population. Growth data are based on subsequent recaptures and remeasurements of these marked individuals (*e.g.*, Hamilton, 1934 and 1955; George, 1940; Raney and Ingram, 1941; Raney and Lachner, 1947; Blair, 1953; Pearson, 1955 and 1957; Fitch, 1956a and 1956b; Jameson, 1956; Martof, 1956; and Turner 1957). The snout-vent (or snout-urostyle) length is usually measured and is difficult to determine accurately. Ryan (1953) and Hamilton (1955) made several measurements of each individual and used a mean value, achieving greater accuracy. Pearson (1955) showed that some other

<sup>1</sup> Contribution No. 16 from the Department of Biology, Wayne State University, Detroit, Michigan.

TABLE I.—Features of growth rates of anurans as revealed by 14 studies of natural populations (all sizes in millimeters and approximate — may represent average or central value of entire range).

Worker	Species	Locality	Maximum size ♂	Maximum size ♀	Size at transformation	Growth to hibernation	1st full season following transformation	2nd full season	3rd full season	Time to sexual maturity ♂ (year after transformation)	Time to sexual maturity ♀ (year after transformation)
Force (1933)	<i>Rana pipiens</i>	Michigan	80?	80?	32	5?	10	7	—	4	4
Ryan (1953)	<i>Rana pipiens</i>	New York	82	92.5	25	22	20	16?	slight	1-2	1-2
Raney & Ingram (1941)	<i>Rana catesbeiana</i>	New York	—	155	45	8	40	30	15	2-3	2-3
Ryan (1953)	<i>Rana catesbeiana</i>	New York	—	—	52	10+	45	—	—	2	2
George (1940)	<i>Rana catesbeiana</i>	Louisiana	171	184	40	29	60	25?	—	2	2
Ryan (1953)	<i>Rana clamitans</i>	New York	90	98	32	22	31	slight	—	1-2	1-2
Martof (1956)	<i>Rana clamitans</i>	Michigan	103	105	32	6	28	17	5.5	1-2	1-2
Turner (1957)	<i>Rana pretiosa</i>	Wyoming	61	72	16	9	10	6.5	5.5	4	5-6?
Hamilton (1934)	<i>Bufo terrestris</i>	New York	—	—	10	20	40	18?	slight	3?	3?
Raney & Lachner (1947)	<i>Bufo terrestris</i>	New York	100	115	10	—	70+	5?	slight?	2	2
Blair (1953)	<i>Bufo valliceps</i>	Texas	—	—	10	—	9	slight	—	1	1?
Hamilton (1955)	<i>Bufo quercicus</i>	Florida	26+	30+	7.5	11	9	—	—	1	2
Pearson (1955)	<i>Scaphiopus holbrookii</i>	Florida	77+	71+	10	—	32	8	3	1-2	1-2
Jameson (1956)	<i>Hyla regilla</i>	Oregon	44?	—	14	7	14	—	—	1	—
Fitch (1956a)	<i>Gastrophryne olivacea</i>	Kansas	37?	42	15	5-13*	11-5*	—	—	1-2	1-2
Bannikov (1950)	<i>Bombina bombina</i>	Near Moscow, Russia	—	56?	17	5	13	10	slight	2	2

\* Two different broods.

TABLE II.—Growth during the first and second years following transformation and its relationship to maximal size in 10 anuran species

Species	Difference between maximum size and size at transformation (mm)	Growth by end of first full year after transformation	% of total growth	Growth by end of second full year after transformation (mm)	% of total growth
<i>Rana pipiens</i>					
(Force, 1933)	48	15	31	22	46
(Ryan, 1953)	60	42	70	58?	97?
<i>Rana catesbeiana</i>					
(George, 1940)	138	89	65	114?	83?
(Raney & Ingram, 1941)	105	48	46	78	74
<i>Rana clamitans</i>				slightly more	?
(Ryan, 1953)	62	53	85		
(Martof, 1956)	72	34	47	51	71
<i>Rana pretiosa</i>					
(Turner, 1957)	50	19	38	26	52
<i>Bufo terrestris</i>					
(Hamilton, 1934; Raney & Lachner, 1947)	97	60	62	78?	80?
<i>Bufo quercicus</i>					
(Hamilton, 1955)	20	19	95		
<i>Hyla regilla</i>					
(Jameson, 1956)	30?	21	70?		
<i>Gastrophryne olivacea</i>					
(Fitch, 1956)	25	17	68	21	84
<i>Scaphiopus holbrooki</i>					
(Pearson, 1955)	64	32	50	8	63
<i>Bombina bombina</i>					
(Bannikov, 1950)	38?	18	46	28	74

body dimension may be used as an index of growth. He calculated growth rates of *Scaphiopus holbrooki* from measurements of the width of the head, and related this dimension to increase in body length.

#### RESULTS OF STUDIES OF NATURAL POPULATIONS

Table I summarizes features of growth in anurans revealed by 14 studies of natural populations.

*General patterns of growth.*—Because of the different sizes of the species involved, it is impossible to compare the absolute increments of growth. However, a proportion may be derived to permit comparison. If a "maximum" size, expressing the approximate limit of growth, is established for members of each population (a mean value when there is marked sexual dimorphism), the difference between this value and the average size at transformation approximates the maximal amount of growth. Growth for any given period may then be expressed in comparable terms, as percent of total growth. The patterns of growth exhibited are diverse, but because the forms in-

volved represent 6 different families of anurans this variation is not surprising (Table II). In the American toad the transformation size (ca. 10 mm) is small when compared to the maximal size (over 100 mm), but in the population of *Rana clamitans* studied by Ryan (1953) the transformation size (32 mm) is about 1/3 of the maximal adult size (90-98 mm). Hence, while the significance of the interspecific comparisons in Table II is uncertain, it is pertinent to compare the growth of members of different populations of the same species. Just why there is such variation in growth rates in different populations of *Rana pipiens*, *R. catesbeiana*, and *R. clamitans* is not presently known, though the roles of temperature and length of growing season are undoubtedly important. George (1940) showed that in Louisiana populations of *Rana catesbeiana* the tadpoles require but one season to transform (as opposed to 2 or 3 in New York), and that post-metamorphic growth and the attainment of sexual maturity are comparably accelerated in the south. It is tempting to ascribe this condition simply to differences in duration of growing season. However, Wright's (1932) data imply that *Rana clamitans* grows more rapidly and to a greater size in New York than in Florida.

These problems resemble those encountered in studies of the developmental rate of anuran embryos and larvae from different populations of the same species. Most of the comparisons of embryonic and larval development in conspecific populations have involved *Rana pipiens* (Moore, 1944; Volpe, 1954, 1957b; Ruibal, 1955), but several species of toads have also been studied (Volpe, 1953, 1957b). The above workers have shown that there are differences in the developmental rate of embryos and larvae, apparently associated with varying temperature regimes or other environmental factors (e.g., rate at which temporary breeding sites dry). As far as postmetamorphic growth is concerned, those adaptations governing rate of development at varying temperatures are most pertinent. The basic idea, when temperature adaptations are involved, is that the embryos of cold-climate populations (i.e., those at high latitudes or high altitudes) are adapted to develop relatively rapidly in cold water (12-15°C), while embryos of warm-climate populations mature relatively more rapidly at water temperatures around 25-30°C. However, at least one cold-climate population has been studied, the embryos of which do not show this sort of adaptation (Ruibal, 1955:333). Here it appears that the whole mechanism of development is retarded by lower temperatures with no counteracting adaptation. These features of embryonic and larval development are reviewed here because of the likelihood that postmetamorphic growth may be similarly influenced (see also Volpe, 1957c:360). However, temperature adaptations related to postmetamorphic growth are not apt to be as striking as those shown to be involved in embryonic development. In most anuran populations the eggs and larvae are the stages in the life cycle against which selective forces operate most rigorously. Because there has been no pertinent experimental work on postmetamorphic growth only speculation is possible. Probably some variable anuran species are adapted for rapid

growth and sexual maturation even in cold climates. Other species may grow at rates simply correlated with temperature and length of growing season. What little is known of bullfrog populations seems to fit this picture.

Future investigations might involve the transplanting of marked individuals from one population to another population of the same species existing under different environmental conditions. A comparison of the growth of the transplants with the members of the undisturbed population might afford clues as to the interaction of the genetic and environmental determiners of growth rate.

In any event there are two extreme patterns of growth (Fig. 1). Most of the growth may take place during the same season as transformation (e.g., *Rana clamitans* in New York, *Bufo quercicus* in Florida, *Bufo valliceps* in Texas), with much smaller increments added in successive years. Or the early growth may be more modest and the later increments, though smaller than the initial growth, are not as drastically reduced as in the preceding examples (e.g., *Rana pipiens* in Michigan and *R. pretiosa* in Wyoming).

*Sexual maturation.*—The time of sexual maturation is of importance in evaluating the reproductive potential of a population of known age composition. Some ambiguity is associated with the term "sexual maturity," for the phrase has been used both to indicate actual

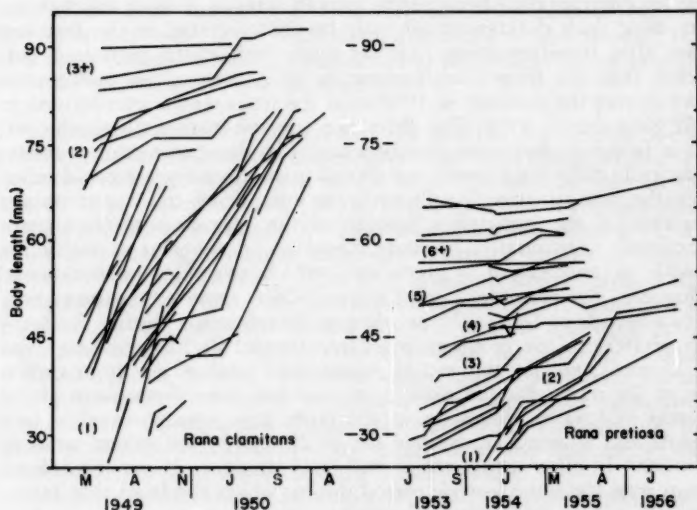


Fig. 1.—Growth rates in *Rana clamitans* and *Rana pretiosa*. Growth records of marked individuals are portrayed as revealed in studies extending over 3 and 4 seasons respectively. Figures in parentheses indicate age-classes. (From data in Ryan, 1953, and Turner, 1957.)

participation in breeding activities and to imply the presence of mature gametes in the gonads. Table I indicates the time at which breeding activities are commenced. The year after transformation is recorded—not the chronological age, which is ordinarily less by 3 to 6 months. Some studies revealed that the first breeding activity might occur in either the first or second season after transformation. In rapidly growing species these differences are associated with the time of transformation, *i.e.*, early or late in the growing season. However, in *Rana pretiosa* in Yellowstone Park, where the pre-reproductive life span is so long that slight age differences within the same year-class are unimportant, differences in time of first breeding in females probably are due to variation in the rate of maturation (Turner, 1957).

*Variation in growth during different growing seasons.*—It has been assumed that, in the same population, anurans of any given age grow a specific amount in one growing season. If workers have suspected, for example, that growth might be exceptionally fast one year and unusually slow the following year, such feelings have been unexpressed because of the difficulty in establishing such differences. It is almost impossible to attack this problem by comparing a limited number of individual growth records. The amount of inherent individual variation is apt to be greater than minor size differences caused by fluctuations in environmental conditions; hence large samples must be available for comparison. Because the growth rates of mature anurans are very slow, such differences can only be demonstrated in the first few years after transformation. In my work with *Rana pretiosa* I suspected that the frogs transforming in 1953 grew a few millimeters more during the summer of 1954 than the frogs which transformed in 1952 grew during 1953. The difference was not statistically significant, but in future studies some attention might be directed to this problem. Drastically differing climatic conditions in successive years could influence the rate of growth sufficiently to complicate the apparent age structure of the population insofar as the year-class size-limits are concerned. Ordinarily, however, there is an inherent capacity for growth in anurans of a given age, which overrides environmental influence. For example, Fitch (1956a, 1956b) reported on the growth of two broods of *Gastrophryne olivacea* transforming during the summer of 1954. One group of frogs transformed in June (average size *ca.* 15 mm), and by the end of August had attained an approximate size of 26 mm. By the middle of October these frogs were about 28 mm in length. Members of the other group transformed in late August and attained an average size of 22 mm by the second week in October. In other words, the second (and younger) group grew about 7 mm over the same 6-week period during which the frogs that transformed in June grew about 2 mm.

*Seasonal rate of growth.*—Studies of growth during one growing season have shown that, except in *Scaphiopus holbrooki*, most growth occurs during one period of the season. This has been most clearly

demonstrated by Martof (1956) for *Rana clamitans* and Turner (1957) for *R. pretiosa*. Martof showed that growth is most rapid during July and that the seasonal growth rate is positively correlated with the number of hours above 60°F. Similarly, in *R. pretiosa* from about 33 to 50 percent of the seasonal growth occurs during a two-week period in July. Ryan (1953) found a comparable condition in young *R. clamitans* in New York, but concluded that the growth of the oldest frogs occurred in the beginning of the growing season. Also, in the *Gastrophryne* observed by Fitch, the frogs transforming in June grew about 11 mm in the 7 weeks following transformation, while those transforming in August grew only 7 mm in the 7 weeks following their transformation. Fitch attributed these differences to the higher midsummer temperatures under which the former group developed. Jameson (1955) stated at one point that *Syrrophus marnocki* grows "faster through the fall and winter months," and in another that "the rate of growth was found to be greater in the spring and summer months. . . ." The latter statement seems more correct. Such variation is the rule even when there is no winter hibernation. *Rana catesbeiana* grows throughout the winter in Louisiana but at a reduced rate (George, 1940). Pearson (1955) concluded that the growth rate of *Scaphiopus holbrooki* in Florida is not influenced by the time of year. This unusual condition is probably associated with the habits of these toads. Pearson points out that the toads remain in their burrow most of the time, emerging to feed only about 30 times a year, and that such excursions occur with equal frequency at any season. Possibly these forays are so brief that seasonal differences in the environment do not influence growth rate.

*Differential growth of the sexes.*—In general, for anuran species studied, the females attain larger sizes than the males (Table I). However, different populations of the same species may vary in this respect. For example, Ryan (1953) found clear-cut size dimorphism in the New York population of *Rana clamitans*, but Martof (1956) maintained that in Michigan there are no maximal size differences between males and females. The time at which size differences first appear varies. In New York, marked differences in male and female *R. clamitans* are apparent during the first season following transformation (Ryan, 1953). The same is true of *Gastrophryne olivacea* in Kansas (Fitch, 1956a), and some other forms. However, Turner (1957) could not demonstrate significant differences in the mean size of 4- and 5-year old male and female *Rana pretiosa*. Furthermore, the males of *Scaphiopus holbrooki* are larger than the females, so size dimorphism does not always involve larger females.

Size dimorphism may arise simply as a result of more rapid growth by the larger sex (Ryan, 1953; Pearson, 1955; Fitch, 1956a). However, if one sex outlives the other, the oldest (and largest) members of the population will be of the same sex. The possible contribution of differential mortality to size dimorphism has been suggested by Turner (1957).

*Individual variation.*—Variation in the growth rates of individuals of the same age has been revealed in all previous studies of anuran growth. Hence, the size-limits of any one age-class may be quite broad—especially in the youngest individuals. Some of this spread represents differences in size at transformation or slight differences in age within the same age-class (resulting from differences in time of transformation). For example, the size of one-year old *Rana catesbeiana* and *R. clamitans* may vary as much as 30-40 mm (based on data of Ryan, 1953; George, 1940). However, even in a cohort of frogs or toads of identical age and size a certain amount of variation in size would soon obtain. *Rana pretiosa* in Yellowstone Park transforms during a few weeks in August and early September (thus minimizing age differences in any one age-class) and the extreme sizes of the early age-classes differ by only about 10 mm (Turner, 1957). The size-limits of some of the early age-classes in ranids are indicated in Table III.

In general the total range of size within the age-classes seems to decrease with greater age, but this impression may be the result of bias in analysis. Anderson (1954) pointed out that *Gastrophryne carolinensis* transforms from May until October, producing an initial age-class of considerable range in size the following spring. However, he stated that this effect seems to be diminished in older individuals, implying that individuals tend to approach more closely a modal size with greater age.

*Growth rate and population density.*—Population density may influence growth. Pearson (1955) showed significantly different growth rates in two populations of *Scaphiopus holbrooki* of different density. The more dense population grew more slowly. This problem has not been investigated by other workers, and in just what manner greater densities operate to slow growth is not known. The retardation may

TABLE III.—Limits of size in 4 species of the genus *Rana* during the first 2 to 4 years following transformation as revealed by studies of 6 natural populations (when two ranges are given, one is early in the growing season, the other later in the same season).

Species	Age-class size-limits (mm)			
	1	2	3	4
<i>Rana pipiens</i> (Force, 1933)	35- 50?	52- 61?		
<i>R. clamitans</i> (Ryan, 1953)	33- 60 40- 73	72- 79 76- 82	83- 90 84- 90	
<i>R. pretiosa</i> (Turner, 1957)	20- 30 23- 32	30- 39 30- 40	37- 45 38- 46	46- 49 45- 50
<i>R. catesbeiana</i> (George, 1940)	44- 82 101-120	101-133		
(Raney & Ingram, 1941)	67- 90	82-110	113-126	125-139
(Ryan, 1953)	55- 92 64- 90			

be simply the result of intraspecific competition for food. Whether slight variations in density within *one* population (associated with contagious dispersion) might contribute to individual variation within the same population is not known.

*Loss of length.*—Apparent loss of length has been reported by almost all investigators of anuran growth. This problem is an unavoidable consequence of measuring the body length of an animal as pliable as a frog or toad. Such apparent losses appear more commonly in larger individuals. Raney and Lachner (1947) found apparent shrinkages to be relatively common in large toads, and Martof (1956) and Turner (1957) encountered similar results in work with *Rana clamitans* and *R. pretiosa*. Ryan (1953), who performed 3 measurements and averaged them, reported few cases of loss of length; this supports the conclusion of Raney and Lachner that such "losses" are the result of errors in technique. However, Martof suggested that the apparent loss of length in green frogs (most commonly between October and April) might be associated with changes in the condition of the frog related to hibernation—especially if measurements of body length were made from the tip of the snout to the anterior lip of the cloaca instead of to the end of the urostyle. In *Rana pretiosa* it was found that apparent losses were more common in males of breeding age, and occurred between May and some subsequent time in the season (Turner, 1957). If a dimension other than the snout-urostyle length of a frog is actually measured, one might expect some "shrinkage" of breeding males following nuptial activities.

#### DISCUSSION

Volpe (1957c), in discussing studies of anuran population (including individual growth rates) comments:

There are few precise and detailed studies of these factors in natural populations. In the literature may be found an array of desultory field observations, much of which cannot be integrated into a comprehensive picture.

There is considerable truth in these remarks. A clear-cut rationale for studies of anuran growth has been largely lacking, although Cagle (1956) has set forth a general program for amphibian life history studies.

If we wish to describe growth, as it occurs under natural conditions, I see no feasible alternative to studies of natural populations. Large enclosures might be used (see Pearson, 1955) but the use of cages or fences always introduces an element of artificiality, which is most extremely expressed in records of the growth of pets (*e.g.*, Cowan, 1941; Wilson, 1950). However, well-designed experiments could be of value in studies of growth, especially in determining the influence of such factors as age, sex, population density, temperature, food supply, etc. The experiments should be replicated with subjects from *one* population, with provisions for control of environmental variables. In field studies individuals should be marked by a tattooing device as

described by Kaplan (1958, 1959). Toe-clipping is not always reliable, especially when studies of several years' duration are involved. There is always some regeneration of excised toes, sometimes enough to cause uncertainties. Even more serious, toes are lost accidentally; unmarked individuals may appear to be marked and marks may be changed owing to such losses. There is a tendency to explain what appears to be exceptional growth as resulting from misidentifications. Emphasis should be laid on the accumulation of a large number of individual growth records. Three measurements involving different frogs will be more instructive than the mean of three measurements of the same individual. The somewhat improved accuracy of the latter technique does not justify the additional time necessary.

Aside from the theoretical value of growth rates, there are two ends served by such information. The first of these is predicated on what might be called the descriptive approach, and is of interest to the population ecologist—namely the age structure and effective breeding size of a population and the fluctuations in these attributes. Information on the attainment of sexual maturity, differential growth of the sexes, and individual variation is subservient to, and contributes to, the major problem: that of describing the age composition of the population and its breeding structure. Such parameters as survival rate, reproductive potential and rate of population growth may then be estimated. The second end is related to causal aspects of growth. Here growth rate and its variations are part of a larger picture involving the influence of age, sex, population density, temperature, food supply and other environmental factors.

#### SUMMARY

The growth rate of anurans, maximal size, and the time at which sexual maturity is attained may vary between different populations of the same species. In some populations studied most of the growth takes place within a year or two after transformation; after this time growth is slight. At the other extreme are species in which the post-metamorphic growth is spread out over some years, so that the annual increments are not so markedly reduced. Seasonal variation in growth is the rule, even when the growing season is not interrupted by hibernation. Size dimorphism probably arises as a result of differential rates of growth by the sexes. Some populations of the same species may show size dimorphism, others not. Variation in the size of anurans of the same age arise because of differences in time of transformation (within the same season) and because of individual variation in growth rates.

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## A Study of *Eleocharis*, Series *Ovatae*

DONALD J. DRAPALIK and ROBERT H. MOHLENBROCK

*Southern Illinois University, Carbondale*

In his latest treatment of the genus, Svenson (1957) subdivided *Eleocharis* into eight morphological series, the fourth being Series *Ovatae*. Members of this series are cespitose annuals or rarely perennials that possess smooth, biconvex achenes that are glistening brown when mature, with compressed lamelliform tubercles, and 2- to 3-cleft styles.

Svenson (1927, 1939, 1957), in his monographic studies, maintains four species, with three of them (*E. obtusa*, *E. ovata*, and *E. engelmanni*) from Illinois. The fourth species, *E. lanceolata*, with ovoid, acute scales and lanceolate spikelets, is apparently not found in Illinois. In addition, the bristleless *E. engelmanni* f. *detonsa* is cited from Illinois.

Gilly (1946), in his work on Iowa Cyperaceae, noted that intergrading forms occur between *E. obtusa* and *E. engelmanni*, even to the extent that typical achenes of both may be found on the same specimens. He felt that the two taxa should not be considered distinct species, but that *E. engelmanni* should be considered a variety of *E. obtusa*. He therefore proposed *E. obtusa* var. *engelmanni*. Fernald (1950), Jones (1950), and Gleason (1952) have maintained *E. obtusa*, *E. engelmanni*, and *E. ovata* distinct in Illinois.

Svenson (1953) in his detailed work on the *obtusa-ovata* complex states that many intermediate forms do exist where the variations come in contact or where unusual environments persist. He also stresses the need for further investigation within this group.

While studying the genus *Eleocharis* in Illinois, it became apparent to the authors that specimens determined previously as *E. obtusa*, *E. engelmanni*, and *E. ovata* were part of a confusing complex. As a result of this, analytical studies of morphological characters of these specimens were carried out. This paper presents these data, and through the interpretation of these data, offers a systematic treatment of these taxa.

### ANALYSIS OF CHARACTERS

*Eleocharis obtusa*, *E. engelmanni*, and *E. ovata* share several characteristics in common. They are all cespitose annuals which range from 3-50 cm tall, with spikelets ovoid or oblong, obtuse to acute, 2-16 mm long, with appressed scales ovate or oblong, with similar coloration. The achenes are obovoid, smooth, yellow or deep brown, 0.9-1.0 mm long.

In their extreme conditions, all three entities appear rather distinct. *Eleocharis obtusa* has ovoid or rarely oblong spikelets which are obtuse to acute. The achenes average 0.9 mm long and 0.8 mm wide, with a tubercle which averages 0.3 mm long and 0.6 mm wide.

The width of the tubercle is more than two-thirds the width of the achene, while the height of the tubercle is more than one-fourth the height of the achene. The bristles are longer than the tubercle, or rarely lacking.

*Eleocharis engelmanni* has oblong or rarely ovoid spikelets which are obtuse to acute. The achenes average 1.0 mm long and 0.8 mm wide, with a tubercle which averages 0.2 mm long and 0.7 mm wide. The width of the tubercle is more than two-thirds the width of the achene, while the height of the tubercle is one-fourth, or less than one-fourth, the height of the achene. The bristles may be lacking or as long as the achene.

*Eleocharis ovata* has ovoid or very rarely oblong, acute or rarely obtuse spikelets. The achene averages 1.0 mm long and 0.7 mm wide, with a tubercle which averages 0.3 mm high and 0.4 mm wide. The width of the tubercle is two-thirds, or less than two-thirds, the width of the achene, while the height of the tubercle is usually about one-fourth the height of the achene. The bristles range from longer than the achene to completely lacking.

The figures obtained in this study for the taxa above are similar to those cited by Svenson (1953).

Specimens which may be considered intermediate are those with the tubercle one-fourth or less than one-fourth the height of the achene and more than one-half the width of the achene with bristles overtopping the achene. The spikelets are ovoid or oblong, obtuse to acute, with achenes averaging 1.0 mm long and 0.8 mm wide, with tubercles averaging 0.2 mm long and 0.6 mm wide.

#### SUMMARY AND CONCLUSIONS

Achene size of all taxa considered in this study is essentially the same. On the average, achenes of *E. obtusa* are slightly shorter, while achenes of *E. ovata* are slightly narrower. Tubercles of *E. obtusa* and *E. ovata* are usually higher than those of *E. engelmanni* and the intermediate specimens. Tubercles of *E. ovata* are narrower than those of the other taxa.

The tubercles of *E. obtusa* are more than one-fourth the height of the achene while those of *E. engelmanni* and the intermediate specimens are one-fourth or less than one-fourth the height of the achene. The tubercles of *E. ovata* are two-thirds or less than two-thirds the width of the achene, while the tubercles of the other taxa are wider than this.

The bristles of *E. engelmanni* never exceed the achene and tubercle, while the bristles of the other taxa sometimes may exceed them. It does not seem feasible to recognize the bristleless form because of the variability of the bristles in this series.

Spikelet shape and scale shape appear to be of little taxonomic significance.

Because of the great variation shown by the intermediate specimens, it seems best to treat *E. engelmanni* as a variety of *E. obtusa*.

The first available varietal epithet of *E. engelmanni* is *detonsa* A. Gray. Since we do not feel that var. *detonsa* (meaning bristleless) is distinct from typical *E. engelmanni*, a new combination for all material of *E. engelmanni* must be made. It would be:

**Eleocharis obtusa** (Willd.) Schultes var. **detonsa** (A. Gray)  
Drapalik & Mohlenbrock, comb. nov.

*Eleocharis obtusa* and *E. ovata* are almost identical in appearance except that *E. ovata* has narrower tubercles and generally a smaller, ovoid, acute spikelet. Because of these seemingly tenuous characters, it seems best to relegate *E. ovata* to varietal status under *E. obtusa*. The new combination would be known as:

**Eleocharis obtusa** (Willd.) Schultes var. **ovata** (Roth)  
Drapalik & Mohlenbrock, comb. nov.

#### KEY TO ILLINOIS ELEOCHARIS, SERIES OVATAE

- A. Tubercle more than two-thirds the width of the achene; bristles longer than the tubercle to lacking.
  - B. Tubercle one-fourth to one-half the height of the achene; bristles longer than the achene, or rarely wanting ..... *E. obtusa* var. *obtusa*
  - B. Tubercle up to one-half the height of the achene; bristles as long as or longer than the achene, or lacking ..... *E. obtusa* var. *detonsa*
- A. Tubercle one-half to two-thirds the width of the achene; bristles usually longer than the tubercle ..... *E. obtusa* var. *ovata*

#### ABERRANT INDIVIDUALS

A specimen collected by Virginius H. Chase (No. 138), identifiable as *E. obtusa* var. *detonsa*, possesses spikelets that are enlarged and flattened at the apex, and tri-cleft as well as simple. A specimen collected by Abney, Dillard, and Mohlenbrock (No. 156), identifiable as *E. obtusa* var. *detonsa*, possesses a dichotomously branched spikelet, as well as simple ones.

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## The Pancreatic Islets of Desert Rodents

W. B. QUAY

University of California, Berkeley

During a recent study of the endocrine organs of the collared lemming, *Dicrostonyx*, a relatively low pancreatic alpha : beta cell ratio was noted in this arctic rodent. It was discovered also that comparative data on the pancreatic islets of rodents in the literature are extremely meager. It seems likely that in at least some species, modifications or specializations in carbohydrate metabolism or utilization associated with climatic adaptations, may be related to modifications in the endocrine glands, especially the pancreatic islets. A survey of the microanatomy of the islets in some North American desert rodents reported here tends to support this belief and contributes data on trends within the Heteromyidae.

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### MATERIALS AND METHODS

Approximately 60 specimens, primarily rodents of the family Heteromyidae, were trapped alive in California and Nevada at different seasons and autopsied after death under ether or chloroform anesthesia either immediately after capture or after varying periods of time in captivity. Rapid autolysis of the pancreatic cells after death necessitates immediate fixation of the tissue and prohibits the use of snap-trapped specimens. Pieces of pancreas were fixed in the following fluids for the times indicated: (1) Helly's fluid, without acetic acid, and neutral formalin mixed 9:1 at time of use, 8 or 15 hours (Thomas, 1937); (2) Bensley's (1911) "acetic-osmic-bichromate," 24 hours; (3) Lane's (1907) "alcohol-chrome-sublimite," 4 or 24 hours; (4) 70 per cent ethanol, 24 hours; (5) 9:1 mixture of neutral formalin:isopropanol, 24 hours; (6) 10 per cent neutral buffered formalin (aqueous) (Lillie, 1954), 1 or more months; (7) Bouin's fluid (75 parts saturated aq. picric acid:25 parts formalin:5 parts acetic acid), 24 hours. The tissues were subsequently embedded in paraffin, sectioned at 7 microns, and stained by the following procedures: (1) Bensley's (1911) "neutral gentian"; (2) Gomori's (1941) modification of the azan technique; (3) chrome alum hematoxylin and phloxine (Gomori, 1941); (4) Halmi's (1952) aldehyde fuchsin; and (5) methenamine silver for argentaffin cells (Lillie, 1954, p. 165). Some of the tissues fixed in neutral buffered formalin were washed in water, embedded in 20 per cent gelatin, cut with a freezing microtome and stained for lipids (oil red O, Lillie, 1954).

## RESULTS

The preservation and staining of the parenchymal cells of the pancreatic islets were evaluated primarily in terms of the cytoplasmic contents of the alpha and beta cells of species of *Dipodomys*, *Perognathus*, *Microdipodops* and the laboratory rat, *Rattus norvegicus* (Long-Evans and mixed strains). Chromophilic cells other than the alpha and beta types were not found in the heteromyid islets. None of the islets' cells were notable in their lipid content; and no sexual differences, nor differences due to captivity or season were apparent in our limited series. In the islets of both rat (*Rattus*) and kangaroo rat (*Dipodomys*) both alpha and beta cells were pink to dull red after Helly's-formalin fixation and staining with methenamine silver. This is not to be considered a positive argentaffin reaction, however. After other fixatives none of the islets' cells showed cytoplasmic staining with methenamine silver. The azan technique after Bouin's fluid fixation, stained alpha cells' cytoplasmic granules yellow to pale orange and those of the beta cells blue-gray. After other fixatives this technique was not successful in differentially coloring the cell types. Neutral gentian stained the cytoplasmic granules of both alpha and beta cells red to purple. But the differential solubilities of the alpha and beta granules in alcoholic and some aqueous fixatives led to similar variations in the rat and the heteromyid sections of pancreas. The beta granules were reduced and the alpha granules were preserved after alcoholic fixatives. The beta granules were selectively demonstrated best after Helly's-formalin and the granules of both cell types were stained after Bouin's fluid. Chrome alum hematoxylin successfully stained the beta cell granules of heteromyids only after fixation in Bouin's fluid or neutral buffered formalin. And the phloxine counterstain of this procedure stained the heteromyid alpha cell granules best after alcoholic fixatives. The best results in differentially staining these cells in heteromyids were obtained with the aldehyde fuchsin technique following fixation in Bouin's fluid. The alpha cells in this instance have orange cytoplasmic granules and a pale greenish-yellow background and the beta cells have intensely purple granules. The staining of the beta granules with aldehyde fuchsin after Helly's-formalin or formalin-isopropanol fixatives is dependent apparently on species differences as well as on quantitative differences. The beta granules are abundant and densely stained in all specimens of *Microdipodops* after these fixatives; they are moderate in abundance and staining in some specimens of *Dipodomys* and *Perognathus*; and they are rarely and weakly stained in *Rattus norvegicus*.

The most immediately obvious distinction of the heteromyid islets is the central, rather than peripheral or scattered, position of the alpha cells. Within the Heteromyidae there are differences in the degree of central clumping of these cells. The most extreme clumping occurs in *Microdipodops*. This is closely approached by that in *Dipodomys deserti*. In other examined species of *Dipodomys* (*heermanni*, *merriami*, *microps*, *nitratoides*, *ordi*, and *panamintinus*) the

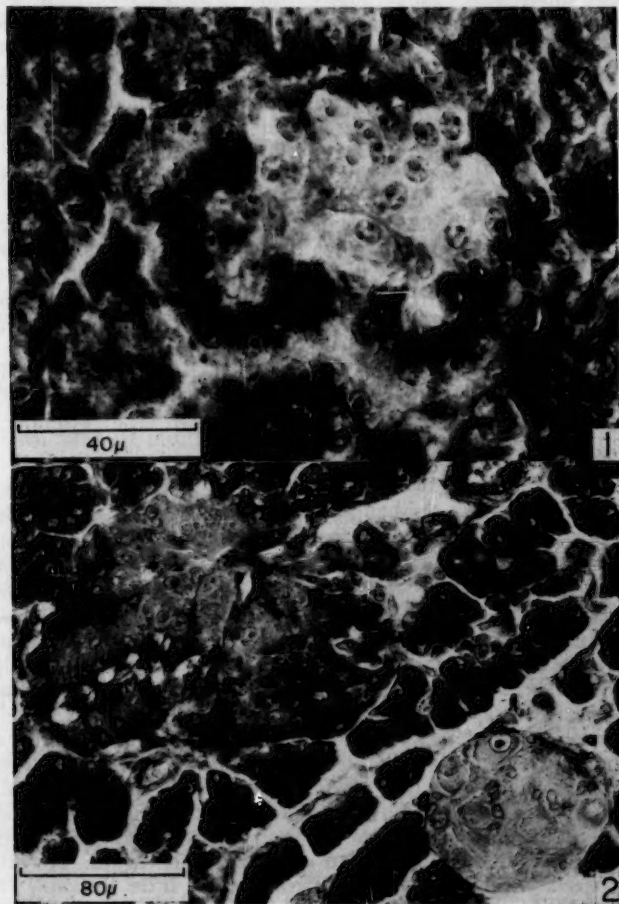
alpha cells, while still primarily central, are either more eccentrically arranged or are in cords among the beta cells. *Dipodomys merriami* most closely approaches the condition in *D. deserti*. Central and partly scattered cords of alpha cells among the beta cells characterize the examined specimens of *Perognathus* (species: *inornatus*, *parvus*, *penicillatus*). The structure of the islets in *Heteromys* and *Liomys*, the remaining genera of Heteromyidae, is not known, nor has it been previously described in other members of the Geomyoidea. However, a single specimen of *Thomomys bottae* fixed in 10 per cent neutral buffered formalin shows scattered alpha cells near the centers of the islets. A specimen of *Ammospermophilus leucurus*, a desert sciurid, shows a similar condition.

In some carnivores it has been shown that the islets of the ventral part of the pancreas lack alpha cells and the dorsal and retro-splenic portion has abundant alpha cells along with the beta cells (Bencosme

TABLE I.—Percentages of alpha cells (1000 chromophil cells counted/animal) in islets of desert rodents stained with Halmi's aldehyde fuchsin technique after fixation in Bouin's fluid (n = number of specimens; x = mean).

Name	n	x	range
Locality			
Heteromyidae			
<i>Microdipodops</i> sp.	3	32.0	29-38
Mono Lake, California			
<i>Dipodomys merriami</i>	3	41.3	37-45
Fletcher, Nev.			
<i>D. panamintinus</i>	1	34.0	
Fletcher, Nev.			
<i>D. heermanni</i>	1	25.0	
Pinnacles, Calif.			
<i>D. deserti</i>	4	24.5	16-33
Trona and Keeler, Calif.			
<i>D. ordi</i>	2	22.5	20-25
Bodie, Calif.; Fletcher, Nev.			
<i>D. nitratoides</i>	1	22.5	
McKittrick, Calif.			
<i>D. microps</i>	3	17.7	15-22
Fletcher, Nev.			
<i>Perognathus parvus</i>	1	41.0	
Lee Vining, Calif.			
<i>P. penicillatus</i>	3	27.0	23-32
Borrego, Calif.			
<i>P. inornatus</i>	1	25.0	
McKittrick, Calif.			
Sciuridae			
<i>Ammospermophilus leucurus</i>	1	28.0	
Inyokern, Calif.			

and Liepa, 1955). The possibility of regional differences in the relative numbers of these cells in the heteromyid pancreas was checked in six specimens by means of counts of islet cells in blocks of tissue from retro-splenic and juxta-intestinal sites. In *Dipodomys deserti* (1 specimen) and *Perognathus penicillatus* (3 specimens) the alpha: beta cell ratio is about the same in the two areas. In *D. nitratoides*



Figs. 1-2.—Pancreatic islets of *Dipodomys* after fixation in Bouin's fluid and staining with aldehyde fuchsin. 1.—Small islet with peripheral beta cells (dark) and central alpha cells; *D. nitratoides* ♀, McKittrick, California. 2.—Medium-sized islet with eccentric mass of alpha cells, upper left, and a ganglion, lower right; *D. deserti* ♂, Trona, California.

and *P. inornatus* on the other hand the retro-splenic pancreas had a higher alpha cell ratio (27 versus 18 per cent, 32 vs. 18 per cent respectively). Since these differences were found in but single animals of each species, their significance may be questioned.

The percentage of alpha cells in comparison with beta cells in the heteromyid islets appears to be high (Table I). And there seem to be species differences, and perhaps parallel evolutionary trends, within the genera *Dipodomys* and *Perognathus*. The antelope ground squirrel (*Ammospermophilus*) also has a high percentage of alpha cells.

Other distinctive characteristics of the heteromyid islets include several features whose significance is difficult to evaluate at this time. A relatively large number of ganglia in the heteromyid pancreas in relation to that of other rodents is one such characteristic (Fig. 2). Cytologically the islets of captive as well as some feral heteromyids are frequently notable for the extreme size of the nucleoli in the chromophils (Figs. 1 and 2). The nucleolar diameters not uncommonly equal or exceed one-half of the nuclear diameters. Inasmuch as nucleolar size has been correlated with the activity of islet cells (Kracht, 1958), heteromyid islets appear to provide unusually interesting material for studies of nucleolar variations and their meaning. Mitoses were seen in two areas of the islets, most commonly along the periphery, and sometimes in the boundary between alpha and beta cellular zones. None of the mitotic cells contained beta granules, and it was uncertain whether a few of them contained alpha granules.

#### DISCUSSION

Among the rodents previously studied the alpha cells are either primarily scattered within the islets (*Cricetus auratus*, *Cavia cobaya*, *Sciurus carolinensis*, *Tamiasciurus hudsonicus*) or are peripheral (*Mus musculus*, *Rattus norvegicus*, *Peromyscus* sp., *Pitymys* sp., *Dicrostonyx groenlandicus*) (Lane, 1907; Thomas, 1937; Hard, 1944; Jewell, 1951; Quay, unpublished observations). Within the Heteromyidae, and perhaps in a considerable number of the Geomyoidea, the alpha cells tend to be central in position, and most markedly so as far as our material is concerned in *Microdipodops*. The fact that these are alpha cells rests on the solubility of their cytoplasmic granules and their staining reactions. In *Ammospermophilus* a more central location of the alpha cells is true in this desert species in contrast to the above previously studied sciurids. Central location for the alpha cells has been noted also in the horse (Gomori, 1939). However, relatively few mammalian taxa have been studied in this regard. Nevertheless the trend within the heteromyids and what little we know from other mammals supports a general correlation between central position of alpha cells and life in an arid environment. The physiological meaning of this, if any, is obscure and may be related possibly to the times of differentiation of the cell types in the fetal or young animal. In the rat (*Rattus*) beta cells differentiate during embryonic develop-

ment and the alpha cells are not recognizable until the second day of postnatal life (Hard, 1944).

The alpha:beta cell ratio is lower in other rodents (*Cricetus auratus* — 19.1 per cent; *Cavia cobaya* — 19.9-22.2 per cent; *Rattus norvegicus* — 5-18 per cent; *Dicrostonyx groenlandicus* — 5.6-16.5 per cent; Müller, 1959; Quay, unpublished) than in the desert species studied here. Among other mammals a high percentage or ratio of alpha cells has been found in the horse (Gomori, 1939) and the few marine forms studied, "seal" (Thomas, 1937) and beluga (*Delphinapterus*) (Quay, 1957). Although the physiological significance of these variations in mammalian islets has remained unstudied and obscure, in some lower tetrapods a relatively high percentage of alpha cells appears to be associated with higher blood sugar levels and greater resistance to insulin (Miller and Wurster, 1959). The alpha and beta cells of the mammalian islets are believed by most investigators to be the sources respectively of the hormones, glucagon (Foa, Galansino and Pozza, 1957) and insulin (Barnett, Marshall and Seligman, 1955), although some controversy persists in regard to glucagon. There appears to be an interrelationship between glucagon and insulin in their actions (De Bodo and Altszuler, 1958). And a hyperglycemic-glycogenolytic activity is usually ascribed to glucagon, but other effects have been noted, including modification of blood cholesterol level (Caren and Carbo, 1956) and blood non-protein nitrogen level (Bencosme, Toledo and Craston, 1959). It has been pointed out, particularly by the Schmidt-Nielsen (1952), that some kangaroo rats (*Dipodomys*) do not need drinking water or moist food and that their production and conservation of metabolic water may be greater from carbohydrate and fatty rather than protein food materials. This information with the islet specializations noted above suggests the value of comparative studies of the significance of the islets and their hormones to the metabolic activities of both young and adult desert rodents.

#### SUMMARY

The microscopic anatomy and cytology of the pancreatic islets in four genera of North American desert rodents (*Dipodomys*, *Microdipodops*, and *Perognathus* of the Heteromyidae, and *Ammospermophilus* of the Sciuridae) were studied after treatments with seven fixatives and five staining techniques. The following characteristics appear to distinguish the islets of some or all of the desert species examined: (1) central clumping of alpha cells, (2) relatively high alpha:beta cell ratio, and (3) preservation and staining of beta cell granules by aldehyde fuchsin following Helly's-formalin and formalin-isopropanol fixatives. Parallel trends within *Dipodomys* and *Perognathus* occur with respect to at least the first two of these characteristics. Other microscopic features and the possible physiological significance of the findings are discussed.

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## Studies on the Larval Morphology of *Ascaris laevis* Leidy, 1856\*

BERT B. BABERO

Southern University A. & M. College, Baton Rouge, Louisiana

Adult nematodes of the genus *Ascaris* Linn., 1758 are seldom found in rodents. Four species are listed by Hall (1916): *A. castoris* Rudolphi, 1809, from *Castor fiber*; *A. laevis* Leidy, 1856 from *Marmota (Arctomys) monax*; *A. pigmentata* von Linstow, 1897, from *Marmota marmota*; *Ascaris* sp., reported by Parona in 1909, from *Mus minutoides*. *Ascaris castoris* and *Ascaris* sp. were inadequately described and *A. laevis* was recently redescribed by Tiner (1951) from specimens obtained from Pennsylvanian and Alaskan woodchucks. Tiner also considered worms identified as *A. columnaris* Leidy, 1856 by Linsdale to be "a variant of *A. laevis*." Because of certain morphological characteristics possessed by *A. pigmentata* which resemble those of the subfamily Anisakinae Railliet and Henry, 1912, Hall felt that this species belonged in another genus. He further suggested that perhaps *Ascaris* sp. and *A. castoris* were erroneously placed. *Ascaris joffi*, from *Citellus pygmaerus* and *A. tarbagan*, from *Marmota sibirica* were described by Schultz (1931). *Ascaris lumbricoides*, genotype, is primarily a parasite of humans and pigs; however, there have been several reports of the accidental occurrence of the species in sciurids (*Sciurus niger*, by Rausch and Tiner, 1948 and by Thomas (cited by Brown and Yeager, 1945); *S. indicus* listed by Baylis, 1939) and murids (*Ondatra zibethica* by Tiner and Chin, 1948).

Specimens of *A. laevis* were collected from several ground squirrels, *Citellus undulatus*, on St. Lawrence Island, Alaska by Dr. L. J. Thomas and the writer. The range of infection was 2 to 4 worms per animal. Because of the infrequent occurrence of members of the genus in rodents and the lack of adequate information relative to the life history of such forms, experimental studies with the species were undertaken. Pathology in experimentally infected hosts due to *A. laevis* was reported by the writer (1959) and a paper on the "tracheal-migration" of the species is in press. The present study on larval morphology is primarily based upon material observed in and recovered from experimentally infected hosts (*Citellus tridecemlineatus*, *C. franklini*, and *Marmota monax*).

### THE EGG

The organization of mature unsegmented ova of *A. laevis* apparently is similar to those of *A. lumbricoides* as described by Martin

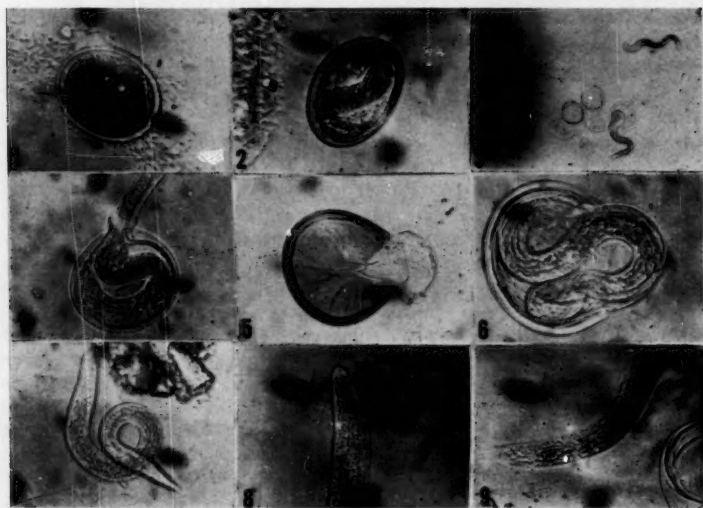
\* Portion of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, University of Illinois. This study was done under Dr. Lyell J. Thomas, whose advice and counsel are gratefully acknowledged. This study was partly supported by a grant from the Arctic Aeromedical Laboratory, Ladd A. F. B., Fairbanks, Alaska.

(1926), Roberts (1934), and Rodgers (1956). The fertilized egg of *A. laevis* is oval in outline with a semi-transparent shell about 3 to 5  $\mu$  thick. The cytoplasm appears to be composed of a large number of granules within a colorless matrix. The nucleus (Fig. 1) is more distinct in fertilized eggs than in non-fertilized ones.

The size of *A. laevis* eggs as given by Tiner (1951) ranged from 0.067 - 0.069 mm in length and from 0.051 - 0.054 mm in width. Of 50 eggs measured by the writer, the length ranged from 0.06 - 0.08 mm, with an average of 0.075 mm, and the width from 0.05 - 0.07 mm, with an average of 0.058 mm.

Embryonation of *A. laevis* eggs was observed to be of typical ascarid development. When teased from the uteri of a mature female worm and incubated at room temperature (25-30° C.) in distilled water, the eggs attained the two-celled stage in less than 24 hours, the morula stage in 4 to 6 days and in 8 to 12 days motile vermiform embryos were seen within the shells. The infective stage was reached by the 17th day (Fig. 2).

By either observing the eggs in the process of being de-shelled in a NaOH-NaCl solution (Elliot, 1954) or by applying slight mechanical pressure to the cover-glass, embryos of *Ascaris laevis* could be



Figs. 1-9.—Photomicrographs showing hatching of second stage larvae of *Ascaris laevis*. 1. A fertilized egg. 2. An embryonated egg. 3-4. Hatched and hatching larvae. 5. Ruptured vitelline membrane left behind in the stained egg-shell. 6. Escaping larva enclosed within the vitelline membrane. 7. Recently hatched larva. 8. Anterior end of larva showing hyaline granules. 9. Posterior part of larva showing hyaline granules. (Figs. 1, 2, 4, and 7,  $\times 800$ ; Fig. 3,  $\times 180$ ; Figs. 6, 8, and 9,  $\times 1680$ .)

released from the egg. Apparently, the egg contains no predetermined place for hatching to occur and rupture seems to take place at a point of least resistance. As the shell splits in a V-shaped manner a portion of the vitelline membrane may extrude through the opening and the embryo escapes after having ruptured the thin membrane at this point. The entire vitelline membrane with the embryo contained in it may escape from the egg, with the young worm becoming completely free of the membrane. Generally, the vitelline membrane is left behind (Fig. 5) when the larva escapes from the shell. Escape appears to be accomplished by the hyper-activity of the organism which apparently produces internal mechanical pressure upon the outer cell wall. The so-called "boring-tooth" described by several investigators for *A. lumbricoides* was not observed for *A. laevis*. The manner in which the worm leaves the egg is not consistent, it may leave tail-first (Fig. 3 and 4), head-first, or even in a U-shaped manner with the mid-body region being freed first (Fig. 6). The moulted cuticle either may be left within the egg-shell or be retained by the larva (Fig. 16). Worms of older egg-cultures appear to leave their shedded cuticles behind more frequently than those from younger ones.

#### DESCRIPTION OF ECDYSIS AND LARVAL STAGES

##### ECDYSIS

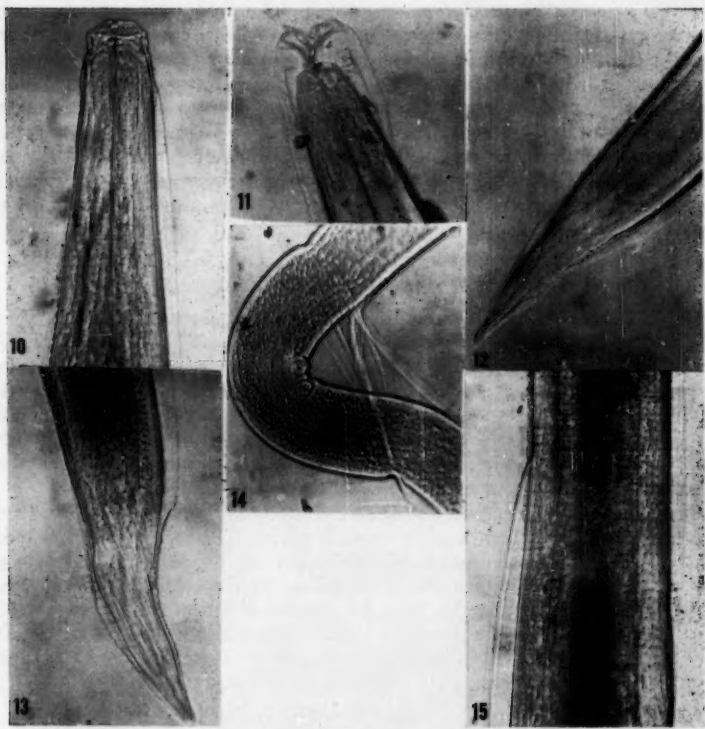
There is considerable inconsistency between nematode groups in the times and patterns in which they moult. Such differences apparently exist within a given species. Much of the knowledge accumulated on this phenomenon has been obtained by the use of chemical materials. Chance observation of a moulting parasitic larva is not common, and frequently the process is neither readily recognized nor understood by the inexperienced investigator. During these studies, the writer was fortunate to have observed ecdysis in several larval stages.

*Ascaris laevis* has five larval stages, each of which except the first is preceded by ecdysis and a growth phase. The first moult within the egg has been mentioned, all others are in the viscera. The second moult takes place within the liver 10 to 12 days after the infection. Casts of discarded cuticles may be recovered from the organ at this time. Third stage larvae remains for a prolonged period of time within the liver and grow slightly. A description of a second stage larva in the process of moulting was recorded as follows:

Worm is retracted. The unsheath cuticle is fitted loosely about the worm, although it is still attached at intervals along most of the body. The cuticle is greatly inflated at the tail-region and the worm is having difficulty in freeing the tail due to the attachment of the cuticle to the rectum. In the labial region, the loosened sheath is pulled far anteriorly but the lining of the esophagus is still attached to the mouth. The worm lashes about freely within the sheath apparently trying to free the mouth attachment.

The third ecdysis probably takes place either while the organism is enroute to the lungs or shortly after it gets there (between 34 to

73 days after the infection). In a few cases this moult may occur in the liver. When early fourth stage larvae (worms which recently moulted) are found in the lungs, late-fourth stage larvae (worms which will soon moult) may be found in the intestine. Ecdysis by fourth stage larvae also was observed and a composite description of the process is presented. The cuticular sheath is duplicated and soon becomes inflated in a blister-like manner about most the worm (Figs. 10, 12 and 15). Labial, esophageal, and tail papillae become greatly modified—the lips become bluntly rounded, but the labial papillae interrupt their



Figs. 10-15.—Photomicrographs showing process of ecdysis by late fourth stage larvae of *Ascaris laevis*. 10. Anterior end of worm. Cuticle has been pulled in to form a hood-like structure about the lips; 11. Anterior end of worm. Cuticle was extended in advance of the labial region but the esophageal lining is still attached; 12-13. Posterior end of worms. Tail regions were distorted and the cuticle inflated to resemble caudal alae. 14. Region of vulva. Worm tried to exsheath through a longitudinal split in old cuticle. 15. Mid-body region of worm. Showed inflation of cuticle. (Figs. 10, 12, 13, 14, and 15,  $\times 200$ ; Fig. 11,  $\times 1000$ .)

contour; the esophagus appears more slender and somewhat extended; the tail becomes greatly attenuated posteriorly (Figs. 12 and 13). The loosened cuticle about the labial region may be pulled in by the worm to form a hood-like structure about the lips (Fig. 10), or may extend far in advance of the lips, although maintaining attachment to the esophageal lining (Fig. 11). The sheath about the tail is greatly inflated to resemble large caudal alae, but attachment to the rectal lining persists for some time. Eventually, the sheath ruptures longitudinally in the region of the second quarter of the body to free this portion of the worm and ultimately allows complete unsheathing (Fig. 14).

#### LARVAL STAGES

*Second Stage Larvae.*—A recently hatched larva is long, slender, and encased in a close-fitting delicate cuticular membrane, which is not yet striated (Figs. 7, 16). The anterior end of the worm is bluntly rounded (Fig. 8) and the posterior end (Fig. 9) gradually tapers. The body is completely filled with hyaline granules<sup>1</sup> which are somewhat more abundant in the region of the intestine (Fig. 16). The lip region is conspicuous, being set-off slightly from the rest of the body. The lips themselves, however, are not yet formed but the cuticle in the labial region is fitted into a three-parted assemblage. The indistinct esophagus, not sharply delimited from the intestine, is slightly rhabditiform with its greatest width near the esophageal-intestinal juncture. The excretory pore can be seen but the nerve ring is not yet discernible. The heavy granulation about the esophagus (Fig. 8) prevents further visibility of structures within this region. The genital primordium is not discernible. The anus, situated ventrally, is recognized by an oblique slit in the cuticle near the posterior end of the body. Of 50 worms measured from five egg-cultures, the length ranged from 0.14 - 0.32 mm, with an average of 0.25 mm. The maximum width is more or less uniform and averaged, 0.02 mm. The length of the esophagus ranges from 0.07 - 0.09 mm, with an average of 0.08 mm. The excretory pore is 0.04 - 0.05 mm from the anterior end, with an average of 0.04 mm. The indistinct anus is 0.02 - 0.03 mm from the posterior end, with an average of 0.02 mm.

Second stage larvae in the liver of an experimental host shows slight modification in morphology three days after parasitizing with embryonated eggs. The body of such larva is long and slender (Fig. 17). A distinct body space can be seen. The labial region forms a

<sup>1</sup> Chitwood (1950) classified the intestinal cell inclusions as either food reserves or waste products. The hyaline granules, considered to be food reserves, in the intestine of ascarids were referred to as "zymogen granules" and were considered to be associated with the synthesis and decomposition of glycogen. Clark (1955) identified the cell inclusions (considered to be waste products), stronglylin, from *Strongylus* spp. and rhabditin, from *Rhabditis strongyloides* as beta zinc sulfide and xanthine, respectively. L. J. Thomas (personal communication) feels that the hyaline granules in larvae of *A. laevis* may be one of the two products identified by Clark.

knob-like structure which is clearly delimited from the rest of the body. Hyaline granules are distributed throughout the length of the worm but are more concentrated in the region of the intestine than in the esophageal and tail areas. The esophagus is short and muscular but still somewhat concealed by granules. The nerve ring is not discernible. The excretory pore is prominent. Measurement of ten "3-day-old larvae" show a length ranging from 0.28 - 0.39 mm, with an average of 0.36; a width of 0.02 mm; an esophagus length from 0.08 - 0.10 mm, with an average of 0.09 mm; and a distance of the anus from the posterior end from 0.02 - 0.03, with an average of 0.02 mm.

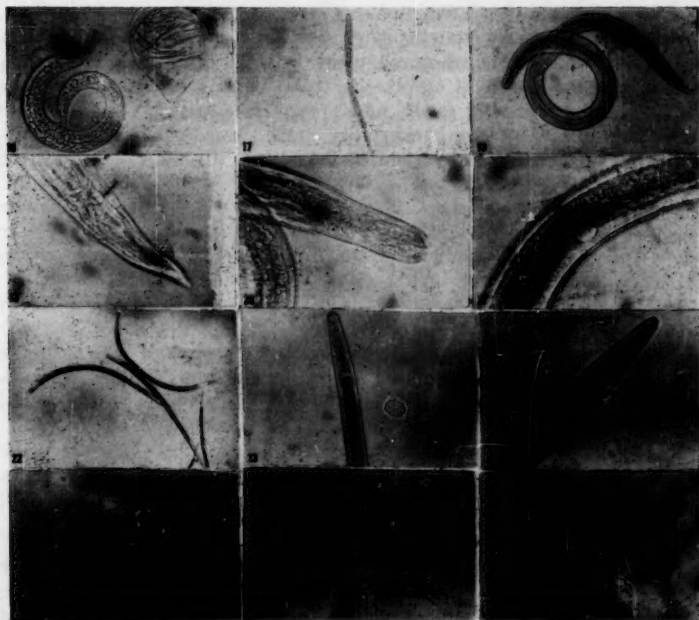
By the 17th day, most larvae increased in length. The lengths of 30 worms studied ranges from 0.37 - 0.87 mm, with an average of 0.63 mm. The body cuticle of such a larva contains vague striations. The labial region begins to show the lip pattern of the adult. The esophagus is clearly visible and has lengthened proportionately with the body. The nerve ring is not distinct but can be distinguished. The excretory pore, duct and cell are visible; the latter is situated near the esophagus. The prominent excretory columns occupy much of the body space. The intestine still has more granules than the tail and esophageal regions. The anus is discernible and the tail tapers sharply.

*Third Stage Larvae.*—Study of about 200 third stage larvae (Fig. 18) showed that generally they can be distinguished from second stage larvae by the following characteristics: (1) the body is longer and more cylindrical; (2) the cuticle is distinctly striated; (3) narrow lateral alae extend the length of the body; (4) the lips are slightly more defined and contain papillae which are vaguely discerned (Fig. 20); (5) the filariform esophagus, nerve ring, and excretory duct, are prominent; (6) the genital primordium can be seen (Fig. 21); (7) gland-like cervical cells (possibly arcade cells) are present about the anterior esophageal area; (8) there is a reduction in the number of granules, especially about the esophageal and tail regions; (9) the anal lips, rectum and rectal glands are visible (Fig. 19); (10) the hexagonal-shaped intestinal cells, each of which contains a basophilic nucleus, can be seen.

Sizes of third stage larvae show a wide variation. The length ranges from 0.09 - 1.40 mm, with an average of 1.04 mm; the width from 0.03 - 0.06, with an average of 0.05 mm; the esophagus, which in some specimens may still be partially concealed by hyaline granules, has a length which averaged about 0.02 mm; the nerve ring, discernible in most larvae despite some granulation in the area, is located between 0.07 - 0.08 mm from the anterior end of the esophagus, with an average of 0.07 mm; the excretory pore is 0.10 - 0.11 mm from the anterior end of the body, with an average of 0.10 mm; the anus, which leads inward to a cuticularized rectum, is situated 0.05 - 0.07 mm from the tip of the tail, with an average of 0.06 mm. The long straight intestine which occupies most of the body is filled with yellowish-brown particles of ingesta, which makes this portion of the body

appear darker in contrast with the esophageal and tail regions. The genital primordium is ventral and in the third quarter of the body. The excretory columns extend posteriad throughout the body. The conical tail curves dorsally.

**Fourth Stage Larvae.**—Study of 15 early fourth stage larvae revealed that differences between these worms and late third stage ones are not apparent without detailed morphological comparisons. Size is not a criterion since there may be some over-lapping. The obvious characteristics which distinguish early fourth stage larvae are: (1) the



Figs. 16-27.—Photomicrographs of second, third, early and late fourth stage larvae of *Ascaris laevis*. 16. Recently hatched second stage larva. Moulted cuticle can still be seen at anterior end of worm. 17. Second stage larva collected from liver three days after experimental feeding. 18. Third stage larva. 19. Posterior end of third stage larva showing rectal glands. 20. Anterior end of third stage larva showing incompletely developed lips. 21. Body region of third stage larva showing genital primordium. 22. Several early fourth stage larvae collected from lungs. 23. Anterior end of early fourth stage larva showing indistinct esophagus, excretory columns, and portion of intestine. 24. Anterior end of late fourth stage larva with lips set-off from body. 25. Labial region of late fourth stage larva showing lips and some papillae and muscular esophagus. 26. Posterior end of late fourth stage female showing pointed tail. 27. Portion of body of late fourth stage larva showing rudimentary vulva. (Figs. 16, 19, 20, 21, 25, and 27,  $\times 1000$ ; Figs. 17, 23, 24, and 26,  $\times 200$ ; Fig. 18,  $\times 800$ ; Fig. 22,  $\times 59$ .)

possession of cuticular annulations; (2) the almost complete absence of hyaline granules in the esophageal and tail regions (Figs. 22, 23); (3) the greater amount of space occupied by the excretory columns; (4) the vagueness of the intestinal cells; (5) the more completely developed lips with their prominent labial papillae; (6) the recognition of sex (the male, by its papillated tail; the female, by its rudimentary vulva). Generally, the esophagus, nerve ring, excretory pore, excretory duct, and excretory cell is more pronounced than in earlier stages since there are fewer granules present to obscure observation of these structures. Early fourth stage larvae are more often found in the lungs than in the intestine.

The size of early fourth stage larvae are as follows: length, 1.40 - 2.20 mm, with an average of 1.70 mm; maximum width, 0.05 - 0.08 mm; length of esophagus, 0.10 - 0.27 mm, with an average of 0.23 mm; nerve ring from the anterior end, 0.05 - 0.12 mm, with an average of 0.09 mm; excretory pore from the anterior end, 0.07 - 0.16 mm, with an average of 0.12 mm; distance of anus from posterior end, 0.06 - 0.08 mm, with an average of 0.07 mm.

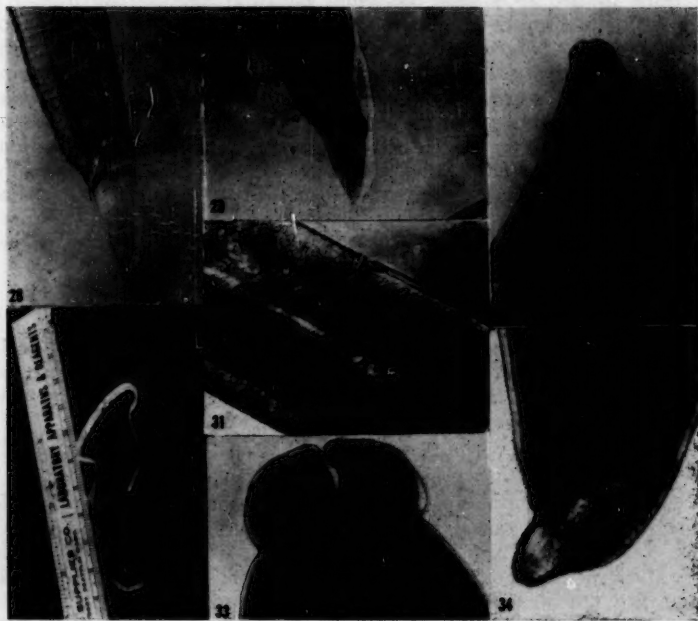
Late fourth stage larvae show considerable variation and are readily distinguished from early fourth stage worms. These larvae are always found in the small intestine. They may be characterized by (1) a large size, (2) lips which are set-off from the body and which nearly resemble those of the adult (Figs. 24, 25), (3) a strongly muscularized esophagus, (4) the absence of hyaline granules, and (5) the greater advancement of sex differences—the tail of the male is bluntly rounded with prominent papillae; the female has a rudimentary vulva (Fig. 27) and in some of the larger specimens genital tubules are present. The tail of the female is sharply tapered (Fig. 26).

The size of late fourth stage larvae varies considerably, some measurements are as follows: total length, 2.80 - 16.40 mm; maximum width, 0.09 - 0.34 mm; length of esophagus from the anterior end, 0.39 - 0.97 mm; anus from the posterior end, 0.09 - 0.27 mm.

*Fifth Stage Larvae.*—Advanced development of reproductive organs, prominent lips being less in diameter than the rest of the body, the close proximity of cuticular annulations, a strongly cuticularized and muscular body, and the more anterior level of the nerve ring and excretory pore primarily serve to distinguish these worms from those of the earlier stage. Size is not always a reliable character since there may be some over-lapping with worms of the late fourth stage. The following description is based upon a composite study of six worms recovered from ground squirrels and woodchucks.

*Male:* The stout cuticle is distinctly striated with numerous annulations (Figs. 28, 30) which appear prominent in the anterior half of the worm and in the tail region. The body musculature is distinctly polymyarian. Three cuticularized lips, sharply set-off from the body and each possessing well-defined papillae, are present. The esophagus is highly muscularized (Fig. 30) with radially directed

fibers which present a transversely striated appearance when the worm is studied morphologically. The esophagus is wide near the labial region but tapers posteriorly for a short distance before assuming a club-shaped appearance. The greatest diameter of the esophagus is at the region of the bulb. The nerve ring is vague in outline but its location is recognizable by groups of sensory ganglia concentrated about 0.32 mm from the anterior end of the esophagus. The ventrally situated excretory pore opens into the cuticle from an obliquely directed canal which is concealed posteriorly by muscle cells, nerve ganglia, and mesenteries. A wide intestinal lumen extends a slightly irregular course from the esophagus to the cloaca. Within the intestine are large brownish particles of ingesta which presents a granular appearance to the organ. The anus, approximately 0.30 mm from the posterior end, is almost ventral and leads inward from an obliquely directed sub-triangular rectum to the cloaca (Fig. 28). Rectal glands are not as prominent as in the two earlier stages of the parasite. Dor-



Figs. 28-35.—Photomicrographs and photographs of immature and mature adults of *Ascaris laevis*. 28. Posterior end of immature male (lateral view). 30. Anterior end of immature adult showing prominent lips and a strong muscularized esophagus, and excretory nucleus. 31. Portion of body showing the vulvular region of an immature adult female (lateral view). 32. Mature adult. 33. Lips of mature adult (lateral view). 34. Posterior end of mature female (dorso-lateral view). (Figs. 28, 29, 30, 32, 33, and 34,  $\times 200$ ; Fig. 31,  $\times 1000$ .)

sally and immediately anterior to the anal opening are two short spicules lying in spicular pouches which unite to become continuous with the cloaca (Fig. 29). Details of the secondary reproductive structures cannot be discerned with accuracy. The tail region posterior to the anus contains tactile papillae which appear slightly stalked. On the blunt part of the tail are three pairs of tandem papillae. A fifth pair of sensory structures is apparently adanal in position. Pre-anal papillae, less prominent and perhaps a little smaller than ad- or postanal papillae, extend irregularly cephalad. Forty-seven pairs of papillae can be counted with certainty.

*Female:* The labial and esophageal regions are similar to those of the fifth stage male. The tail region is without papillae but possesses irregularly distributed phasmids (chemo-receptors). The tail is more bluntly rounded than that of male specimens. The vulva is ventral and located about 3.83 mm from the anterior end of the body. It leads inward to a short muscular cuticularized vagina (Fig. 31) which, for a distance of about 0.23 mm, extends slightly oblique toward the tail. Subsequently, the vagina bends posteriad at a right angle and bifurcates from the vaginal trunk to differentiate into thin-walled, slightly muscularized uteri which extend caudally for about 1.50 mm. At this distance the distal part of each uterus gives rise to a long tube-like ovary which coils extensively in a posteriad direction.

Size variation of fifth stage female larvae is as follows: total length, 24.70 - 32.40 mm; maximum width, 0.42 - 0.59 mm; length of esophagus, 1.77 - 3.75 mm; nerve ring from anterior end, 0.28 - 0.35 mm; excretory pore from anterior end, 0.29 - 0.37 mm; vulva from anterior end, 3.76 - 3.91 mm; anus from posterior end, 0.30 - 0.33 mm.

#### SPECIAL FEATURES OF THE ADULT AND SYNONYMY

With few minor variations the morphology of mature adult specimens of *A. laevis* as studied by the writer fits the redescription of the species as given by Tiner (1951). Two additional features which may be of diagnostic value are discussed below.

#### THE LIPS

Characteristic of the genus *Ascaris* is the presence of three cuticularized lips, one dorsal and two ventro-lateral (Figs. 33 and 35). The greatest size of the former in an average-sized adult of *A. laevis* (Fig. 32) measures 0.35 mm in width and 0.25 mm in length. The latter lips are about equal measuring 0.29 mm wide and 0.21 mm long. The morphology of the lips are somewhat similar to those of *A. devosi* as described by Sprent (1952). The pulp of each lip has two components, an apical part containing the internal papillae and the basal part containing the external papillae and phasmids. Two sub-oval dark areas comprise the former part, each of which is approximately 0.71 mm long and containing a deep groove extending inward from the mouth. A small papilla is situated at the base of

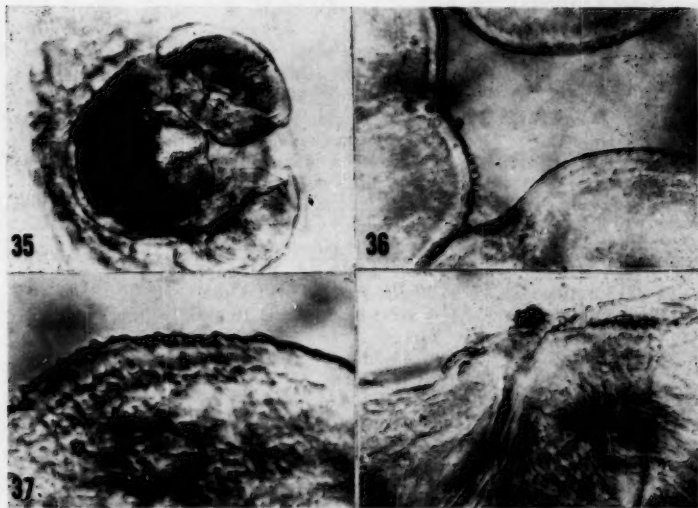
each groove. The pulp of the latter part resembles the musculature of the anterior esophagus. The basal part of each lip contains two pairs of external cuticularized papillae on its outer surface. The papillae on the dorsal lip appear larger than those on the ventrolateral lips. Denticulated processes are irregularly distributed over the oral surface of each lip (Figs. 36 and 37). Those along the inner lip surface are somewhat triangular (Fig. 36) and attain a height of about 0.52 mm. Toward the outer lip surface the denticles gradually assume a dome shape and become smaller until they can be recognized no longer (Fig. 37).

#### THE ANAL REGION

In the pre-and post-anal areas of the male are cuticularized bosses which are irregularly distributed for an equal distance of about 0.04 mm. These cuticular roughenings end abruptly at the anal opening (Fig. 38). It is of interest that this characteristic also was described by Sprent for the ascarid in the fisher and marten, *A. devosi*.

#### SYNONYMY

A comparative examination of the description and illustrations of *Ascaris tarbagan* described by Schultz (1931) from a Siberian wood-



Figs. 35-38.—Photomicrographs showing views of lips and anal region of adult worms. 35. En-face view of lips. 36. En-face view of lips showing denticles. 37. En-face view of portion of dorsal lip showing shape and distribution of denticles. 38. Lateral view of cloaca showing peri-anal roughenings. (Fig. 35,  $\times 200$ ; Fig. 36,  $\times 1,000$ ; Figs. 37, and 38,  $\times 1,680$ .)

chuck (*Marmota siberica*) and later reported from an Alaskan woodchuck (*Monax monax ochracea* Swarth) by Phillip (1938) reveals that this species is co-specific with *A. laevis* as redescribed by Tiner and as studied by the present writer (Table I). It is therefore suggested that *A. tarbagan* be considered a synonym of *A. laevis*. It is conceivable that *A. laevis* (syn. *A. tarbagan*) in ground squirrels of St. Lawrence Island, Alaska is of Siberian origin, since few mammals are indigenous to the island. *C. undulatus*, the host from which the writer's material was originally collected, is widely distributed in Asia. A detail discussion of the occurrence of this ground squirrel in Siberia is given by Ognev (1947).

TABLE I.—Some morphological comparisons in millimeters between *Ascaris laevis* and *A. tarbagan*

Characters	<i>A. laevis</i> (Tiner, 1951)	<i>A. tarbagan</i> (Schultz, 1931)	<i>A. laevis</i> (present study)
Females			
Total length	80-100; 135*	92-169	78-139
Maximum width	2.40-2.60	1.73-2.60	1.70-2.50
Esophagus			
length	4.50-5.10	3.48-4.64	4.20-5.10
width	0.59-0.71	0.91	0.42-0.62
Nerve ring from			
anterior end	0.75-0.90	—	0.52-0.74
Excretory pore from			
anterior end	1.12-1.16	0.83-0.88	0.78-0.98
Vulva from			
anterior end	20-28	17-36	19-32
Anus from			
posterior end	0.58-0.83	—	0.57-0.76
Egg-size			
length	0.07	0.07-0.08	0.06-0.08
width	0.05	0.07	0.05-0.07
Males			
Total length	30-48; 72*	57-65	42
Maximum width	1.2-1.8	1.16-1.37	0.94
Esophagus			
length	2.45-3.64	3.30-3.40	3.89
width	0.32-0.50	0.43-0.50	0.32
Nerve ring from			
anterior end	0.44-0.55	0.66-0.68	0.40
Excretory pore from			
anterior end	0.63-0.75	0.71-0.79	0.57
Anus from			
posterior end	0.38-0.41	0.43-0.46	0.41
Spicule length	0.36-0.55; 0.41-0.54*	0.38-0.56	0.36

\* Measurements obtained from *C. beecheyi* specimens, which Tiner considered to be a "variant" of *A. laevis*.

## SUMMARY

The morphology of the larval stages of *Ascaris laevis* Leidy has been described, as well as certain anatomical features of the adult worm. Some observations on the development and hatching of the eggs of the parasite and ecdysis by several larval stages have been discussed. *Ascaris tarbagan*, from *Marmota siberica* was considered a synonym of *A. laevis*.

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## Observations on the Offshore Benthic Flora in the Gulf of Mexico off Pinellas County, Florida<sup>1</sup>

R. C. PHILLIPS and V. G. SPRINGER

Florida State Board of Conservation Marine Laboratory<sup>2</sup>  
Maritime Base, Bayboro Harbor, St. Petersburg

The Floridian Plateau is that projection of North America which separates the deep water of the Atlantic Ocean from the deep water of the Gulf of Mexico (Vaughan, 1910). According to Cooke (1945) the Plateau includes both the State of Florida and an equally great or greater area that lies submerged in water less than 50 fathoms deep. Gunter (1929) called this submerged portion the Florida Shelf. The shelf width in the vicinity of Pinellas County is approximately 105 miles. The offshore slope is gradual in certain areas and at a distance of 40 miles offshore in the Gulf of Mexico the bottom may be under approximately 100 feet of water.

The present report contains a discussion of the benthic algal flora collected 9-20 miles offshore at depths from 35-60 feet. It is not known if attached algae occur to the offshore edge of the shelf, however, the fact that they are found so far offshore is significant. It is probable that algal growth will be found at distances further offshore and in water deeper than investigated at the present.

Several papers contain information on the marine algae of the Gulf coast of Florida. These are: Taylor (1928, 1936, 1954, 1954a), Nielsen and Madsen (1949, 1949a), Madsen and Nielsen (1950), Humm (1953), and Earle (1956). Humm (1956) listed algal records from inshore and offshore waters in an unpublished general checklist of the St. Georges Sound-Apalachee Bay region in northwest Florida. Excepting Humm (1956) and Taylor (1928), all the other papers cited here concern work confined to bay and close-shore waters.

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<sup>1</sup> Portions of this paper were read at the Twenty-fourth Annual Meeting of the Florida Academy of Sciences, 20 February 1960.

<sup>2</sup> Contribution No. 43.

## METHODS AND MATERIALS

The reef areas were located with the aid of a fathometer. SCUBA-type diving equipment was used in collecting, and thus we believe that adequate sampling was made at most stations. The first few collections are doubtfully representative as the perfection of the use of the diving gear was of prime concern. Algae collected by the junior author were incidental to the collection of fishes, but usually a concerted effort was made to obtain a thorough sample. The importance of the use of SCUBA equipment cannot be overemphasized, for it represents the contrast between visual observation and the aimless wanderings of the collecting dredge. Collection periods of one-half hour to two hours were allowed with the use of the diving equipment.

A small chipping hammer was used at times to aid in the removal of the more firmly attached plants. While in the water the collected algae were retained in a small-mesh nylon bag. Preservation was made in ten per cent formalin upon return to the boat.

Eight collections were made in 35 - 40 feet depths and 12 in 45 - 60 feet depths during a one year period. The collections have been lumped into these two depth ranges, owing to the assemblage of plants found in each. It is possible that further study will reveal a "continuum" of plant distribution from shallower depths to the deeper depths rather than the sharp difference in floral composition that is now evident.

Upon return to the laboratory the algae were identified and mounted on herbarium sheets for permanent retention in the Laboratory's herbarium. Thirty of the microscopic forms were unfortunately discarded after the identification (footnoted in Table II).

## DESCRIPTION OF THE HABITAT

Most of the stations were located 240° (magnetic) off Johns Pass, Madeira Beach. Some stations were made at 230°, 235° and 245° off Johns Pass, and one station was located 70° off the southern tip of Egmont Key, approximately 9 miles offshore. The 35 - 40 feet depths were located approximately 9 - 12 miles offshore, and the 45 - 60 feet depths were located approximately 13 - 20 miles offshore.

Three types of substrates were encountered. The first, a flat, shelly and sandy bottom, was generally unproductive, but this bottom type at one location at a depth of 40 feet was found to support a network of *Caulerpa sertularioides*. Collecting was not done on this type of bottom, owing to its general unproductiveness. The second type substrate, an artificial one, consisted of the metallic wrecks of ships. This type was observed to be receptive to algal colonization, and macroscopic red algae were much more abundant on these structures than on rocky reefs. The third type substrate, limestone reefs with heavy incrustations, supported an abundant and varied algal flora. These reefs rise on the average from three to four feet above the rubble and sandy bottom. Most of the collections were made on these reefs. Dr. Robert N.

Ginsburg described a sample of this limestone as a dolomitic calcarenite, possibly of Tertiary age. The area covered by individual reefs varied from a few hundred square feet to an estimated several thousand square feet.

The reefs occur in depths from about 15 feet at one-half mile offshore to a depth and distance as yet undetermined. Operators of fishing party boats report the sporadic occurrence of reef type silhouettes on their fathometers to distances of at least 50 miles out. Jordan (1952) reported a distinctive reef formation 100 miles northwest of Tampa Bay in depths of 18 - 30 fathoms. It is possible that these reefs are an extension of the same formations which we studied.

The reefs in the 15 feet depths were not studied because the turbidity of the water limited visibility to but a few feet or less.

The area surrounding those reefs studied was always covered by a very fine silt which was easily disturbed and would obscure the area, requiring several minutes to clear. This silt was more abundant at the shallower depths. Rubble of shell and pieces of limestone surrounded the reefs. A very soapy type limestone was once noticed under this rubble.

A portion of the material incrusting a reef was examined in the laboratory. The structure was found to consist of an unknown black organic crust overlying a pink crust of *Lithothamnion syntrophicum* which was in cystocarpic state. This algal crust was solid but was also present as flecks to a depth of 4 mm from the surface. Other organic material found in the upper 4 mm were: filamentous red and blue-green algae, bryozoans, and worm tubes. In some parts the rock was riddled by the tubes of polychaetous annelids and pholadids. Major incrusting forms on the reefs also included the mollusks *Arca* and *Spondylus*, and a number of alcyonarians and small hard corals.

Bottom detritus was dissolved in nitric acid. A residue remained which consisted of sand-like particles 105 - 210 $\mu$  in diameter, with a few particles ranging from 1300 - 1400 $\mu$  in diameter. A very minute portion of the residue appeared to be organic in nature.

Although no Secchi disc readings were made, it was observed that the water was always much clearer in the 45 - 60 feet depths than in the 35 - 40 feet depths. This is related to the more abundant accumulation of silt around the reefs in the shallower depths and the fact that deeper waters are less subject to turbulence. Lateral visibility in the shallower depths was estimated to be about 10 - 20 feet. Once during a period of 20 mph northwest winds visibility was less than one foot on the bottom at 35 feet. In depths of 45 - 60 feet the lateral visibility was about 35 - 40 feet and never was as poor as in the 35 - 40 feet depths.

The St. Petersburg Field Station, U. S. Fish and Wildlife Service, initiated monthly hydrographic sampling stations in the Gulf of Mexico west of Egmont Key in October, 1958. Egmont Key is approximately 11 miles south of Johns Pass. Both surface and bottom temperatures, taken during the study, were generously contributed for

use in this paper. During the period of October, 1958, through September, 1959, the month of coldest water was January. In this month the surface reading was 13.7°C. and 15.8°C. in approximately 35 feet of water, 10 miles west of Egmont Key; at 20 miles west of the Key, in approximately 55 feet of water in January, 1959, the surface reading was 15.2°C. and 16.5°C. at the bottom. The warmest month was July, 1959. At 10 miles offshore the surface reading was 30.6°C. and was 30.6°C. in 35 feet of water; at 20 miles offshore the surface reading was 30.2°C. and 30.1°C. in 55 feet of water. The most conspicuous element in this data is the lack of differential between surface and bottom temperatures in both depths throughout the year. The temperatures were taken in the field by a Whitney Thermistor, a continuous recording device. Because of the lack of information on bottom water temperatures in the Gulf of Mexico, the temperatures recorded for the two above described locations will be listed in Table I.

A surface current of about 2 mph was usually present in the area studied. When present the direction of the current was always toward the north.

#### RESULTS

The species list and data are given in Table II. The following abbreviations are used to denote abundance: V—very common, U—uncommon, C—common, R—rare. A blank in this column indicates that no observations were made.

All plants were either attached to the bottom, to other algae, or occurred entangled among other algae.

A total of 158 taxa of algae were obtained. Of these, eight were

TABLE I.—Water temperatures (unpublished data from St. Petersburg Field Station, U.S. Fish and Wildlife Service)

Date	35 feet deep		55 feet deep	
	Surface	Bottom	Surface	Bottom
Oct. 1958	29.0	29.0	29.0	29.0
Nov. 1958	23.0	23.0	24.5	25.1
Dec. 1958	21.5	21.9	22.3	22.6
Jan. 1959	13.7	15.8	15.2	16.5
Feb. 1959	19.4	19.0	21.0	17.0
Mar. 1959	18.7	18.7	20.4	20.1
Apr. 1959	20.7	20.0	20.1	19.4
May 1959	23.9	23.6	23.9	22.0
Jun. 1959	27.9	27.8	27.5	26.6
Jul. 1959	30.6	30.6	30.2	30.1
Aug. 1959	28.9	28.9	29.4	29.8
Sep. 1959	27.9	28.1	28.1	27.8

identified only to genus and one only to the family because the specimens lacked critical taxonomic characters.

Ninety-five taxa were found at the 35 - 40 feet stations, of which seven were identified only to genus. One hundred and eleven taxa were found at the 45 - 60 feet stations of which six were identified only to genus and one only to the family.

Species found only on the metal wrecks are footnoted in Table II. *Caulerpa sertularioides* was found on sand on June 18, 1958. All other collections came from the limestone reefs.

TABLE II.—Species list

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
<i>CYANOPHYCEAE</i>					
<i>Anacystis marina</i> Dr. & Daily <sup>1</sup>	55-60	5-X-58	R	*	
* <i>Calothrix pilosa</i> Harv. <sup>3</sup>	40	7-XII-58	U	*	
* <i>Hydrocoleum penicillatum</i> Taylor <sup>2</sup>	50	2-V-59	C	*	
<i>Lyngbya confervoides</i> C. Ag. <sup>2</sup>	60	9-VIII-58		*	
<i>L. gracilis</i> (Menegh.) Rab.	35	8-II-59	C	*	
	55	31-I-59	V	*	
	55-60	5-X-58	V	*	
<i>L. majuscula</i> Harv. <sup>2</sup>	35	17-VIII-58		*	
	55	7-X-58		*	
	55-60	21-X-58	V	*	
* <i>L. meneghiniana</i> Kutz. Gom.	38	14-II-58	C	*	
<i>L. mitsuii</i> Phillips	40	7-XII-58	V	*	
* <i>L. rosea</i> Taylor <sup>3</sup>	60	9-IX-58		*	
<i>L. sordida</i> (Zanard.) Gom.	35	3-I-59	C	*	
	35	8-II-59	U	*	
	38	14-II-59	U	*	
	40	7-XII-58	U	*	
<i>L. sordida</i> fa. <i>bostrychicola</i> (Crouan) Gom. <sup>1</sup>	55-60	5-X-58	U	*	
<i>Mastigocoleus testarum</i> Lagerheim <sup>2</sup>	38	14-II-59	V		
	55	31-I-59	U		
<i>Microcoleus chthonoplastes</i> (Fl. Dan.) Thur.	40	7-XII-58	U	*	
<i>Phormidium papyraceum</i> (C. Ag.) Gom.	50	2-V-59	C	*	
<i>P. submembranaceum</i> (Ard. et Straff.) Gom. <sup>3</sup>	45-50	23-XI-58	U	*	
<i>Plectonema nostocorum</i> Born.	38	14-II-59	V	*	
	40	7-XII-58	V	*	
	55-60	5-X-58	C	*	

TABLE II.—(continued)

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
<i>Skujaella thiebautii</i> DeToni <sup>3</sup>	45	29-VI-58	C		
<i>Spirulina subsalsa</i> Oerstedt fa. <i>oceanica</i> (Crouan) Gom. <sup>1, 2</sup>	55-60	5-X-58	U	*	
<b>CHLOROPHYCEAE</b>					
<i>Acetabularia crenulata</i> Lamx. <sup>2</sup>	40	18-VI-58			
* <i>Avrainvillea asarifolia</i> Børgs. <sup>1</sup>	55-60	5-X-58			
* <i>A. nigricans</i> Decaisne	55	7-IX-58			
* <i>Bryopsis plumosa</i> (Huds.) C. Ag.	35	7-II-59	R	*	
<i>Caulerpa crassifolia</i> (C. Ag.) J. Ag. fa. <i>mexicana</i> (Sonder) J. Ag.	38 45	14-II-59 29-VI-58	U		
<i>C. crassifolia</i> (C. Ag.) J. Ag. fa. <i>typica</i> (Weber) Børgs.	40 55 55-60	7-XII-58 7-IX-59 5-X-58			
<i>C. cupressoides</i> (West) C. Ag. var. <i>elegans</i> (Crouan) Weber	45-50	23-XI-58	U		
<i>C. paspaloides</i> (Bory) Grev. var. <i>typica</i> Weber.	35	13-VII-58			
<i>C. peltata</i> (Turn.) Lamx.	60 55 55-60 55-60	19-VIII-58 7-IX-58 21-IX-58 5-X-58			
<i>C. prolifera</i> (Førsskal) Lamx.	35	13-VII-58			
<i>C. sertularioides</i> (Gmel.) Howe	40 35 39 40 55 60 55 55-60	18-VI-58 13-VII-58 19-XI-58 7-XII-58 31-I-59 9-VIII-58 7-IX-58 5-X-58		V U	
<i>C. sertularioides</i> (Gmel.) Howe fa. <i>brevipes</i> (I. Ag.) Sved.	38	19-II-59	U		

TABLE II.—(continued)

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
<i>C. sertularioides</i> (Gmel.)					
Howe fa. <i>longipes</i>					
(C. Ag.) Collins	38	19-II-59	U		
	50	2-V-59	R		
* <i>Cladophora glaucescens</i>					
(Griff.) Harv.	35	13-VII-58		*	
<i>Codium isthmocladum</i>					
Vick.	35	8-II-59			
	38	19-II-59	V		
	35	17-VIII-58			
	39	9-XI-58	R		Gametangia
	40	7-XII-58	U		Gametangia
	55	31-I-59	R		
	50	2-V-59	U		
	60	9-VIII-58		*	
	55	7-IX-58			
	55-60	21-IX-58			
	55-60	5-X-58		*	
* <i>C. repens</i> ?					
(Crouan) Vick	35	8-II-59			
	60	25-IV-59	R		
	50	2-V-59	R		
<i>C. taylori</i> Silva	35	8-II-59			
	35	13-VII-58			
	35	17-VIII-58			
* <i>Derbesia vaucheriaeformis</i>					
(Harv.) J. Ag. <sup>1</sup>	35	17-VIII-58	U	*	
<i>Entocladia wittrockii</i> Wille	40	7-XII-58	V	*	
* <i>Ernodesmus verticillata</i>					
(Kutz.) Borgs. <sup>2, 3</sup>	40	7-XII-58	R	*	
<i>Halimeda discoidea</i>					
Decaisne	55	7-IX-58			
* <i>H. opuntia</i> (L.) Lamx.					
var. <i>typica</i> Barton	40	18-VI-58			
	55	27-IV-58	U		
* <i>H. scabra</i> Howe	35	13-VII-58			
	39	9-XI-58	C		
	40	7-XII-58	V		
	55	31-I-59	V		
	58	9-IV-59	V		
	60	25-IV-58	V		
	55	27-IV-58	C		
	50	2-V-59	V		
	48	24-V-59	V		
	60	9-VIII-58	C		Sporangia
	55	7-IX-58			
	55-60	5-X-58			
	45-50	23-XI-58	V		

TABLE II.—(continued)

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
<i>Penicillus capitatus</i> Lamarck <sup>2</sup>	60	9-VIII-58			
	55	7-IX-58			
Unidentified species of Chaetophoraceae <sup>4</sup>	55	27-IV-58	U		
* <i>Rhipocephalus oblongus</i> (Decaisne) Kutz. <sup>2</sup>	40	18-VI-58			
	60	9-VIII-58			
	55-60	5-X-58			
* <i>R. phoenix</i> (E. & S.) Kutz. fa. <i>typicus</i> Gepp.	55	31-I-59			
	58	9-IV-59	C		
	60	25-IV-58	V		
	50	2-V-59	V		
	48	24-V-59	V		
	45	29-VI-58			
	55	7-IX-58			
	45-50	23-XI-58			
<i>Rhizoclonium kernerii</i> Stockmayer	35	8-II-59	R	*	
	55	31-I-59	C	*	
	60	25-IV-59	R	*	
<i>Udotea conglutinata</i> (Solander) Lamx.	40	18-VI-58			
	35	13-VII-58			
	50	2-V-59	U		
	48	24-V-59	U		
	60	9-VIII-58			
	55	7-IX-58			
<i>U. flabellum</i> (E. & S.) Howe	53	11-IV-59	U		
	55	7-IX-58			
	55-60	5-X-58			
* <i>U. spinulosa</i> Howe	50	2-V-59	U		
* <i>Valonia macrophysa</i> Kutz.	60	25-IV-59	U		
	55-60	5-X-58			
<b>PHAEOPHYCEAE</b>					
<i>Dictyopteris</i> <i>delicatula</i> Lamx. <sup>1, 2, 3</sup>	55-60	5-X-58	R		
<i>Dictyota</i> <i>cervicornis</i> Kutz.	55	7-IX-58	R		
	55-60	5-X-58	R		
<i>D. dichotoma</i> (Huds.) Lamx.	50	2-V-59	R		Tetrasporic
	60	9-VIII-58			
* <i>D. divaricata</i> Lamx.	55-60	21-IX-58	R		
	45-50	23-XI-58	C	*	

TABLE II.—(continued)

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
<i>Dictyota</i> sp.	35	13-VII-58	R	*	
	55	7-IX-58	R		
* <i>Dilophus alternans</i> J. Ag. <sup>3</sup>	40	7-XII-58	R		
<i>Ectocarpus duchassaingianus</i> Grun. <sup>2</sup>	40	18-VI-58		*	Pleurilocular sporangia
<i>Ectocarpus</i> sp.	40	18-VI-58	V		
	45	24-VI-58	V		
* <i>Eudesme howei</i> Taylor <sup>3</sup>	40	18-VI-58		*	Sporangia
<i>E. zosteræ</i> (J. Ag.) Kylin <sup>3</sup>	50	2-V-59	R	*	
<i>Padina vickersiae</i> Hoyt <sup>3</sup>	40	18-VI-58			Antheridia & oogonia
<i>Sargassum filipendula</i> C. Ag.	35	3-I-59	V		
	35	8-II-59	C		
	38	14-II-59	V		
	39	9-XI-58	V		
	40	7-XII-58	U		
	55	21-I-59	U		
	55	27-IV-58	C		
	58	11-IV-59	C		
	50	2-V-59	V		
<i>S. filipendula</i> C. Ag. var. <i>montagnei</i> (Bailey) Coll. & Hervey	35	8-II-59	U		
<i>S. hystrix</i> J. Ag. var. <i>buxifolium</i> (Chauvin) J. Ag.	60	9-VIII-58			
	55-60	21-IX-58			
<i>S. lendigerum</i> ? (L.) C. Ag.	58	11-IV-59	U		
	55-60	5-X-58			
* <i>S. vulgare</i> C. Ag.	45-50	23-XI-58	U		
* <i>Spatoglossum schroederi</i> (Mart.) J. Ag.	35	14-II-59	U		
	38	14-II-59	U		
<i>Sphacelaria furcigera</i> Kutz. <sup>3</sup>	45-50	23-XI-58	U		
<b>RHODOPHYCEAE</b>					
<i>Acrochaetium</i>					
<i>aurainvilleae</i> Børgs.	40	7-XII-58	V	*	Monospores
<i>A. flexuosum</i> Vick.	35	3-I-59	C	*	Monospores
<i>A. netrocarpum</i> Børgs.	40	18-VI-58		*	
<i>A. phacelorrhizum</i> Børgs. <sup>3</sup>	55	31-I-59	U	*	
<i>A. seriatum</i> Børgs. <sup>3</sup>	35	8-II-59	V	*	Monospores
	38	14-II-59	C	*	Monospores
<i>A. unipes</i> Børgs.	55	27-IV-58	U	*	Monospores

TABLE II.—(continued)

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
<i>Acrochaetium</i> sp.	35	13-VII-58		*	
	60	25-IV-59	C	*	
	50	2-V-59	C	*	
	45	29-VI-58		*	
<i>Acrochaetium</i> sp.	50	2-V-59	C	*	
<i>Agardhiella tenera</i> (J. Ag.) Schmitz	38	14-II-59	C		
	35	13-VII-58			
	35	17-VIII-58			
	39	9-XI-58			
* <i>Amphiroa fragilis-</i> <i>sima</i> (L.) Lamx.	55	7-IX-58			Cystocarpic
* <i>A. rigida</i> Lamx. var. <i>antillana</i> Børgs.	60	9-VIII-58			
<i>Botryocladia occi-</i> <i>dentalis</i> (Børgs.) Kylin	38	14-II-59	U		
	35	17-VIII-58			
	39	9-XI-58	U		Cystocarpic
	40	7-XII-58			
	48	14-V-59	U		
	55-60	5-X-58	C		
<i>Callithamnion bys-</i> <i>soides</i> Arnott <sup>3</sup>	35	3-I-59	C	*	
	48	31-I-59	U	*	
<i>C. cordatum</i> ? Børgs. <sup>1, 3</sup>	55-60	5-X-58		*	
<i>C. roseum</i> (Roth.) Harv. <sup>3</sup>	55-60	21-IX-58		*	
<i>Callithamnion</i> sp.	35	17-VIII-58		*	
	55	7-IX-58		*	
<i>Ceramium bys-</i> <i>soideum</i> Harv. <sup>2</sup>	40	7-XII-58	V	*	
<i>C. codii</i> (Richards) Mazoyer	35	3-I-59	U	*	
	39	9-XI-58	C	*	
	40	7-XII-58	C	*	Tetrasporic
	55	31-I-59	U-C	*	
	60	25-IV-59	C	*	
	50	2-V-59	V	*	Tetrasporic
* <i>C. corniculatum</i> Mont.	39	9-XI-58	C	*	
	55-60	5-X-58	V	*	
<i>C. deslongchampsii</i> Chauvin <sup>3</sup>	45	29-VI-58		*	
<i>C. fastigiatum</i> (Roth) Harv. fa. <i>flaccidum</i> H. G. Petersen	40	18-VI-58		*	Tetrasporic
* <i>C. floridanum</i> J. Ag.	55-60	21-IX-58		*	
<i>C. subtile</i> J. Ag. <sup>2, 3</sup>	55	31-I-59	C	*	

TABLE II.—(continued)

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
<i>C. tenuissimum</i> (Lyngbye) J. Ag.	35	3-I-59	R	*	
	38	14-II-59	V	*	Tetrasporic
	40	18-VI-58		*	Tetrasporic
	35	13-VII-58		*	
	55	31-I-59	C	*	
	50	2-V-59	U	*	
	48	24-V-59	U	*	
	60	9-VIII-58		*	
	55	7-IX-58	V	*	
<i>Champia parvula</i> (C. Ag.) Harv.	35	3-I-59		*	
	35	8-II-59	R	*	
	40	18-VI-58		*	
	35	17-VIII-58	U	*	
	39	9-XI-58		*	
	40	7-XII-58	U	*	
	50	2-V-59	R	*	
	60	9-VIII-58		*	Cystocarpic
	55	7-IX-58		*	
<i>Chondria dasyphylla</i> (Woodward) C. Ag. <sup>2, 3</sup>	40	18-VI-58			Cystocarpic
<i>Chrysomenia</i> <i>enteromorpha</i> Harv.	50	2-V-59	R		
<i>Crouania attenuata</i> (Bonne.) J. Ag.	35	3-I-59	U	*	Tetrasporic
	60	9-VIII-58		*	Cystocarpic, antheridial
	55	7-IX-58		*	Tetrasporic
<i>Dasyopsis antillarum</i> Howe <sup>3</sup>	38	14-II-59	R		Tetrasporic
<i>Digenia simplex</i> (Wulf.) C. Ag. <sup>2</sup>	60	25-IX-59	U		
* <i>Dudresnaya caribaea</i> (J. Ag.) Setch. <sup>3</sup>	40	18-VI-58		*	Cystocarpic
<i>Erythrocladia sub-</i> <i>integra</i> Rosenvinge	38	14-II-59	C	*	
	40	7-XII-58	C	*	
	55-60	5-X-58	C	*	
<i>Erythrotrichia</i> <i>carnea</i> (Dillw.) J. Ag.	35	3-I-59	R	*	
	35	8-II-59	R	*	
	38	14-II-59	C	*	
	40	18-VI-58		*	
	35	13-VII-58		*	
	40	7-XII-58	R	*	

TABLE II.—(continued)

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
	60	25-IV-59	U	*	
	55	27-IV-58	C	*	
	50	2-V-59	U	*	
<i>Eucheuma ancantho-</i> <i>cladum</i> (Harv.) J. Ag.	35	13-VII-58			
* <i>E. isiforme</i> (C. Ag.) J. Ag.	35	8-II-59	C		Cystocarpic
	38	14-II-59	U		
	35	17-VIII-58			
	39	9-XI-58	R		
	40	7-XII-58	U		
	55-60	21-IX-58			
	55-60	5-X-58			
	45-50	23-XI-58			
<i>Fosliella farinosa</i> (Lamx.) Howe var. <i>solmsiana</i> (Fal-					
kenberg) Taylor <sup>1, 2</sup>	55-60	5-X-58	V	*	
<i>F. lejolisii</i> (Rosanoff) Howe	35	3-I-59	V	*	Cystocarpic
	35	8-II-59	V	*	
	38	14-II-59	V	*	Cystocarpic
	40	18-VI-58		*	
	39	9-XI-58		*	Cystocarpic
	40	7-XII-58	C	*	
	55	31-I-59	V	*	
	60	25-IV-59	V	*	
	50	2-V-59	V	*	
	60	9-VIII-58		*	
	55	7-IX-58		*	
	45-50	23-XI-58	V	*	Cystocarpic
<i>Gelidium pusillum</i> (Stackhouse) LeJolis <sup>1, 2, 3</sup>	55-60	5-X-58			
<i>Goniolithon decutescens</i> (Heydrich) Foslie <sup>2</sup>	60	9-VIII-58			
* <i>G. solubile</i> Foslie & Howe <sup>2</sup>	35	8-II-59	C		
	50	2-V-59	V		Cystocarpic
<i>Goniotrichum alsidii</i> (Zanard.) Howe	38	14-II-59	R	*	
	50	2-V-59	C	*	
* <i>Gracilaria bursa-</i> <i>pastoris</i> (Gmel.) Silva	40	7-XII-58	U		Cystocarpic
* <i>G. cervicornis</i> (Turn.) J. Ag. <sup>1</sup>	55-60	5-X-58	C		Cystocarpic, tetrasporic
<i>G. cornea</i> J. Ag. <sup>2</sup>	60	9-VIII-58			
	55	7-IX-58			

TABLE II.—(continued)

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
* <i>G. curtissiae</i> J. Ag.	60	9-VIII-58			
* <i>G. cylindrica</i> Børgs. <sup>1</sup>	55-60	5-X-58			
<i>G. ferox</i> J. Ag.	38	14-II-59	U		
	40	7-XII-58	U		
	55-60	5-X-58	V		Cystocarpic
* <i>G. mamillaris</i> (Mont.) Howe	35	17-VIII-58			
	40	7-XII-58	U		
<i>G. verrucosa</i> (Huds.) Papenf.	35	13-VII-58			
<i>Gracilaria</i> sp.	38	14-II-59			
* <i>Griffithsia</i> <i>globulifera</i> Harv.	35	3-I-59	R	*	
	35	8-II-59	U	*	
	40	7-XII-58	R	*	
	60	9-VIII-58		*	Tetrasporic
	55	7-IX-58		*	Tetrasporic
	45-50	23-XI-58	R	*	
<i>Grinnellia americana</i> (C. Ag.) Harv. var.					
<i>caribaea</i> Taylor	38	14-II-59	C		Tetrasporic
<i>Halymenia agardhii</i> DeToni	35	13-VII-58			
<i>H. floresia</i> (Clemente) C. Ag.	35	13-VII-58			
	60	9-VIII-58			
	55	7-IX-58			
<i>H. gelinaria</i>	55-60	21-IX-58			
Collins & Howe	39	9-XI-58	R		
	40	7-XII-58	R		
	55-60	21-IX-58			Cystocarpic
<i>H. pseudofloresia</i> Collins & Howe	38	14-II-59	U		
	35	13-VII-58			
	55-60	5-X-58	C		
* <i>Hildenbrandtia</i> <i>prototypus</i> Nardo <sup>2</sup>	60	25-IV-59	C		
	55-60	5-X-58	V		
* <i>Hypoglossum tenui-</i> <i>folium</i> (Harv.) J. Ag.	60	9-VIII-58			Tetrasporic
* <i>Jania adhaerens</i> Lamx.	40	18-VI-58		*	Cystocarpic
	60	25-IV-59	U		
	60	9-VIII-58		*	Cystocarpic
<i>J. capillacea</i> Harv. <sup>3</sup>	40	7-XII-58	C	*	
<i>J. pumila</i> Lamx. <sup>2, 3</sup>	40	7-XII-58	C	*	
<i>Laurencia gemmifera</i> Harv.	50	2-V-59		*	Tetrasporic
	60	9-VIII-58			

TABLE II.—(continued)

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
<i>L. intricata</i> Lamx.	55	7-IX-58			
<i>L. obtusa</i> (Huds.) Lamx.	55	31-I-59			
* <i>L. papillosa</i> (Førsskal) Grev. <sup>2</sup>	38	14-II-59	R		
	60	25-IV-59	C		
	55	27-IV-58	R		
<i>L. poitei</i> (Lamx.) Howe	40	18-VI-58			
	40	7-XII-58	U		
	50	2-V-59	U		Tetrasporic
	45	29-VI-58			
	60	9-VIII-58			
<i>Laurencia</i> sp.	35	8-II-59	R	*	
	35	13-VII-58	R	*	
<i>Lithothamnion</i> <i>occidentale</i> Foslie	60	25-IV-59	C		
* <i>L. syntrophicum</i> Foslie	38	14-II-59	V		Cystocarpic
	60	25-IV-59	C		Tetrasporic
<i>Lophosiphonia</i> <i>scopulorum</i> (Harv.) Womersley	40	7-XII-58	U	*	Cystocarpic
* <i>Melobesia mem-</i> <i>branacea</i> (Esper) Lamx.	55	31-I-59	C		
	55	27-IV-58	U		
* <i>Meristotheca</i> <i>duchassaignii</i> J. Ag. <sup>1</sup>	35	17-VIII-58			
<i>Mesothamnion</i> <i>caribaeum</i> Børgs. <sup>3</sup>	40	7-XII-58	R	*	
<i>Peyssonnelia</i> <i>rubra</i> (Grev.) J. Ag.	38	14-II-59	U		
	55	7-IX-59			
<i>Polysiphonia</i> <i>binneyi</i> Harv.	35	13-VII-58			Tetrasporic
	55	7-IX-58		*	Cystocarpic
* <i>P. denudata</i> (Dillwyn) Kutz. <sup>3</sup>	45	29-VI-58		*	
* <i>P. gorgoniae</i> Harv. <sup>3</sup>	55	31-I-59	U	*	Cystocarpic
* <i>P. hapalacantha</i> Harv. <sup>3</sup>	40	18-VI-58		*	
<i>P. havanensis</i> Mont.	55-60	21-IX-58		*	
	45-50	23-XI-58		*	
<i>P. howei</i> Hollenberg	60	9-VIII-58		*	Cystocarpic
<i>P. macrocarpa</i> Harv. <sup>2</sup>	35	6-I-59	U	*	
	35	8-II-59	R	*	
	38	14-II-59	U	*	
	40	7-XII-58	U	*	

TABLE II.—(continued)

Species	Depth —feet	Date	Abundance	Epiphyte	Reproductive state
<i>Polysiphonia</i> sp.	35	13-VII-58			Tetrasporic
<i>Rhabdonia ramosissima</i> (Harv.) J. Ag.	60	9-VIII-58		*	
	40	7-XII-58	U		Cystocarpic
	55-60	21-IX-58			
<i>Scinaia complanata</i> (Collins) Cotton var. <i>intermedia</i> Børgs.	38	14-II-59	R		Cystocarpic
	40	18-VI-58			Cystocarpic
* <i>Seirospora</i> <i>occidentalis</i> Børgs <sup>1, 3</sup>	55-60	5-X-58		*	Cystocarpic
<i>Spermothamnion</i> <i>gorgoneum</i> (Mont.) Born. <sup>2</sup>	39	9-XI-58	V	*	Polyspores
* <i>S. investiens</i> (Crouan) Vick.	60	9-VIII-58		*	
	55	7-IX-58		*	
* <i>S. investiens</i> (Crouan) Vick. var. <i>cidaricola</i> Børgs.	50	2-V-59	V	*	
<i>Spyridia flamentosa</i> (Wulf.) Harv.	35	3-I-59	R	*	
	35	13-VII-58			
	39	9-XI-58			
	60	9-VIII-58		*	Cystocarpic
	55	7-IX-58	V		
	55-60	21-IX-58			
<i>Wurdemannia miniata</i> (Drap.) Feldmann & Hamel	55-60	5-X-58			

\* Not previously reported north of the Dry Tortugas on the Florida Gulf coast.

<sup>1</sup> Species found only on metal wrecks.

<sup>2</sup> Species found only in very shallow water at the Dry Tortugas [as reported by Taylor (1928)].

<sup>3</sup> Species not in herbarium.

<sup>4</sup> Material examined by Dr. H. J. Humm. The plant does not have setae. Dr. Humm stated that each cell is extended on the top side into a peak or point. No confidence is placed on identification beyond the family.

#### DISCUSSION

A very interesting algal association was noted in the 45 - 60 feet depths where a vast carpet of *Halimeda scabra*, composed of plants two to three inches tall, was found on the reefs. *Rhipocephalus phoenix typicus* was usually associated with the *Halimeda*, but was

not as abundant. *Sargassum filipendula* was also abundant, not on the reef, but on the detritus-covered hard bottom surrounding it. These attached *Sargassum* plants, mostly from two to three feet high, occurred one plant every square meter over very large areas, but on several occasions no plants were found. This association was not seen in the 35-40 feet depths. *Sargassum filipendula* was found at 5 of the 8 stations in 35-40 feet and is considered to be a characteristic plant of these shallower depths. *Halimeda scabra* was found in only 3 of the 8 collections in this depth range and was abundant at only one of these. *Rhipocephalus phoenix* was not found at the 35-40 feet depths, but *R. oblongus* occurred in one collection in which it was associated with *Halimeda opuntia typica*.

Several species of *Goniolithon* and *Lithothamnion* were occasionally observed as large knobby growths on the rocky reefs. It is believed that these crustaceous coralline algae are probably an important constituent of the reef flora, however, due to the lack of attention to these algae, we cannot elaborate on this.

Despite the fact that most collections were made on the limestone reefs, several species of Codiaceous green algae with rhizoidal systems were found, often in great abundance. Plants of *Halimeda scabra* and *Udotea flabellum* were attached directly to the hard rock surface. The other species of this group, viz., *Caulerpa* spp., *Halimeda* spp., *Rhipocephalus* spp., *Udotea* spp., *Penicillus capitatus*, and *Avrainvillea* spp., had extremely fine shell detritus and sand grains bound up in the rhizoids. The reef surface was never smooth, but was extremely pitted and craggy. Detritus and sand evidently collected in the rock depressions and potholes, and these algae which are anchored by rhizoids probably invaded the reefs by growing in the detritus filled depressions.

A large number of algal species were found at the 35-40 feet depths, but excepting *Sargassum filipendula*, none seemed particularly conspicuous. Once during a storm, vast amounts of *S. filipendula* were found floating on the surface over 35 feet of water. These plants had holdfasts and were in a fresh condition. Reefs were present on the bottom in the vicinity of this floating mass, and it is possible that the rough water may have torn the plants loose from the bottom.

Many more species of red algae were found in the 35-40 feet depths than any other group; however, of the macroscopic algae no group appeared to be dominant at a particular station. The epiphytic flora in the 35-40 feet depths was a major constituent of the species. Three species of macroscopic algae supported most of these epiphytes: *Halimeda scabra*, *Sargassum filipendula*, and *Codium isthmocladum*, none of which are red algae.

In contrast to the 35-40 feet depths is the 45-60 feet range in which *Halimeda*, *Rhipocephalus*, and *Sargassum* usually dominated the algal biomass present on the rocky reefs. This excludes consideration of the encrusting coralline red algae. In terms of biomass the

macroscopic reds were very scarce. Species-wise the red algae comprised over half the total.

On two occasions the junior author collected on metal shipwrecks. One wreck was at a depth of 32 - 35 feet and the other was at 60 feet. Although portions of these wrecks rose as much as 20 feet off the bottom, only the algae within two or three feet of the bottom were collected. At both stations the red algae appeared to comprise the major portion of the algal biomass. *Sargassum* was not present about the shallower wreck and only sparse plants of *S. lendigerum* were present around the deeper one. The holdfast type base of the macroscopic red algae appears to be better suited for colonization on hard surfaces such as metal than does the rhizoid type base of the Codiaceous green algae. Wherever ship wrecks are found in the shallow waters of the Gulf of Mexico, red algae should be expected to prevail.

Eleven species are newly reported for Florida. These are: *Sargassum lendigerum* (?), *Acrochaetium avrainvilleae*, *A. netrocarpum*, *A. phacelorhizum*, *A. seriatum*, *A. unipes*, *Callithamnion cordatum*, *C. roseum*, *Ceramium codii*, *Mesothamnion caribaeum*, and *Lophosiphonia scopulorum*. Forty-seven species (marked by an asterisk in Table II) have not been previously reported north of the Dry Tortugas on the Florida Gulf coast and thus represent northward range extensions.

TABLE III.—Synopsis of species

Depth Range (Feet)	35-40	45-60
Total taxa of Cyanophyceae	9	13
Total taxa of Chlorophyceae	21	23
Total taxa of Phaeophyceae	9	12
Total taxa of Rhodophyceae	56	63
TOTAL	95	111
Taxa not found at other depth range	47	63
Taxa found at both depth ranges		48
Taxa of Rhodophyceae not found at other depth range	27	34
Taxa of Rhodophyceae found at both depth ranges		29
Taxa of epiphytes not found at other depth range	27*	31*
Taxa of epiphytes found at both depth ranges		19
Per cent of taxa which were rhodophycean epiphytes	31	31
Per cent of epiphytes which were Rhodophyceae	63	68

\* Four taxa were found in both depth ranges, one was an epiphyte in the 35-40 feet range only, and three were epiphytes in the 45-60 feet range only.

A summary of much of the information obtained in the present study is contained in Table III. The most obvious and interesting conclusion is that despite the differences, species-wise, between the two depth ranges considered, the composition of the algal flora is essentially the same in both. That is, both the ratios of the major algal groupings (Classes) and the ratios of the epiphytes remain constant.

In Table IV we have grouped data reported by Taylor (1928) for comparison with similar data in our Table III. It can be seen that the Tortugas algae also hold, at least in the shallower depths comparable to ours, a more or less constant relationship between the various groupings, though not of the same ratios as ours. These constant relationships at the different depths, although including different species, seem to denote that they are more than just a function of the number of possible species. The factors which might regulate these relationships are unknown to us.

More extensive collecting must be done in order to reveal possible seasonal variation in plant abundance and/or occurrence. The records collected thus far do not indicate such variation.

Taylor (*op. cit.*) recorded only 60 per cent of the taxa listed in Table II from the Dry Tortugas. It is interesting to note that 28 of the taxa we list (footnoted in Table II) were found by Taylor only in much shallower water. It has been the junior author's experience with fishes that several species found locally only in deep water are recorded from very shallow depths at Tortugas. Taylor emphasized the biomass dominance of the green algae in depths comparable to ours, but called attention to the fact that the number (taxa) of red algae greatly exceeded the number of green algae. Our findings are in accord with his.

#### SUMMARY

Marine algae were collected on limestone reefs in water 35-60 feet deep in the Gulf of Mexico off Pinellas County, Florida, over a period of one year. SCUBA type diving equipment was used.

Two depth ranges were chosen, owing to the assemblage of plants found in each. The first was 35-40 feet, and the second was 45-60 feet. Ninety-five taxa were found in 35-40 feet in eight collections. One hundred and eleven taxa were found in 45-60 feet in twelve collections. A total of 158 taxa of plants were found during the study.

TABLE IV.—Comparative data on depth from Dry Tortugas  
(extracted from Taylor, 1928, Table 6)

Depth (meters)	3.1	9.2	18.3	36.6	55	73.2	91.5
Total taxa of Cyanophyceae	2	3	3	3	—	—	—
Total taxa of Chlorophyceae	27	34	24	17	13	10	9
Total taxa of Phaeophyceae	14	17	16	6	1	1	1
Total taxa of Rhodophyceae	52	56	46	24	7	3	—

The red algae, though high in species numbers, were small in biomass in both depths. However, when metal wrecks were encountered, it was observed that the biomass of red algae was large. *Sargassum filipendula*, owing to the regularity with which it was found in 35 - 40 feet, is considered a characteristic plant in this depth range. No other algal complex or species was observed to dominate on the reefs in this depth.

Vast carpets of *Halimeda scabra* were observed at most of the 45 - 60 feet stations. This species was observed to be characteristic of this depth. *Rhipocephalus phoenix* and *Sargassum filipendula* were often associated with *Halimeda*.

The epiphytic flora, a large percentage of which were red algae, accounted for nearly one-half of the total number of species found.

Eleven species are newly reported for the state, and 47 represent northward range extensions from the Dry Tortugas.

On the basis of this study and comparison with the results of Taylor's (1928) work at the Dry Tortugas, a more or less constant relationship between the various algal groupings can be seen. Although different species are included in the two areas, those relationships seem to denote that they are more than just a function of the number of possible species. The factors which might regulate these relationships are unknown to us.

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# Ectoparasites of Pocket Gophers From Colorado

RICHARD S. MILLER

University of Saskatchewan

and

RONALD A. WARD

Walter Reed Army Medical Center

Four species of pocket gopher occur in Colorado — *Cratogeomys castanops* occupies most of the area south of the Arkansas River in Baca, Prowers and Bent Counties and the eastern part of Otero County; *Geomys bursarius* is found throughout most of the plains north of the Arkansas River and east of the front range of the Rocky Mountains; *Thomomys bottae* occurs in the valleys of the southwest, along the front range as far north as Colorado Springs, and from the front range west to Salida; and *Thomomys talpoides* occupies most of the remaining areas (Miller, unpublished).

The ranges of these four species meet in different combinations of contiguous allopatry at various localities along the Arkansas River and in the vicinity of Colorado Springs, thus offering a unique opportunity for studies of their interrelationships. The purpose of this study was a preliminary survey of the ectoparasites of the pocket gophers of Colorado, with special reference to localities where the ranges of the different pocket gophers meet and where host-specificity would best be shown.

## METHODS

Collections were made in August 1957 at localities selected on the basis of the distributions outlined above. The pocket gopher specimens were placed in individual plastic bags and stored with dry ice until they could be examined. The parasites were removed within one or two days after the gophers were trapped, and were treated in the manner outlined by Ward (1957a). Lice and a few mites and fleas were also recovered from museum skins in the Warren Collection at Colorado College, the U.S. Fish & Wildlife Service collection at the Denver Federal Center, the Denver Museum of Natural History, and Colorado State University.

We would like to express our appreciation to the following who identified the parasites and provided information about their habits and distributions: Phyllis Johnson (Fleas), G. M. Kohls (Ticks) and Russell Strandtmann (Mites). The lice were identified by Ronald A. Ward.

## RESULTS

The numbers of ectoparasites and the host species they were collected from are shown in Table I.

TABLE I.—Ectoparasites collected from pocket gophers in Colorado. Values shown are the numbers of individuals of each parasite species collected from each host species, and the number of individuals of the host species (in parentheses) on which the parasite was found.

Ectoparasite Species	<i>Thomomys bottae</i>	<i>Thomomys talpoides</i>	<i>Geomys bursarius</i>	<i>Cratogeomys castaneops</i>
ACARINA				
<i>Macrocheles</i> sp.		1( 1)	1( 1)	
<i>Copropholaspis</i> sp.	1( 1)			
<i>Haemogamasus ambulans</i>	1( 1)	44(13)		1( 1)
<i>Ischryopoda armatus</i>	1( 1)			
<i>Hirstionyssus geomydis</i>	2( 2)	29(10)	1( 1)	
<i>Ornithonyssus</i> sp.		1( 1)		
Phytoseidae		1( 1)		
<i>Garmania ponorum</i>		1( 1)		
<i>Haemolaelaps geomyis</i>	20(12)	76(23)	92(13)	2( 1)
<i>Aulaelaps stabularis</i>		4( 2)		
<i>Ixodes sculptus</i>	10( 2)	91(18)	2( 1)	
<i>Ixodes kingi</i>	9( 2)			
<i>Ixodes</i> sp. <sup>1</sup>	41( 2)	1( 1)		
<i>Dermacentor</i> sp.	1( 1)			
Sarcoptidae		1( 1)		
Listrophoridae			1( 1)	
MALLOPHAGA				
<i>Geomydoecus thomyus</i>		321(73)		
<i>G. chapini</i>		331(67)		
<i>G. californicus</i>	863(50)		122( 7)	
<i>G. minor</i>	655(44)			
<i>G. geomydis</i>				204( 5)
<i>G. geomydis-californicus</i> <sup>2</sup>			351(17)	
SIPHONAPTERA				
<i>Foxella ignota</i>	49(16)	192(60)	35(11)	1( 1)
<i>Dactylopsylla percernis</i>				8( 5)
<i>Thrassis petiolatus</i>	1( 1)			

<sup>1</sup> Unidentifiable larvae; probably a mixture of *I. sculptus* and *I. kingi*.

<sup>2</sup> See text for discussion of integration of *G. geomydis* and *G. californicus*.

A brief account of the habits and host-associations of the ectoparasites is given in the following section:

#### MITES AND TICKS (ACARINA)

##### MACROCHELIDAE

Macrochelid mites occur in soil and on vertebrates and invertebrates. They are probably not parasitic (Baker and Wharton, 1952).

*Macrocheles* sp.—Two females were found on two specimens of *T. talpoides*.  
*Coprophilopsis* sp.—One female was found on *T. bottae*.

##### HAEMOGAMASSIDAE

These mites are common parasites of small mammals throughout the world, which suggests that they may be important in the transmission of plague, typhus, tularemia, and perhaps other diseases (Baker and Wharton, 1952). They attach to the host only to feed; non-feeding time is spent in the nest of the host.

*Haemogamasus ambulans* (Thors.)—This genus is restricted to small, burrowing rodents and insectivores (Ewing, 1929). *H. ambulans* was common on *T. talpoides* and single specimens were collected from *T. bottae* and *G. castaneus*.

*Ischyropoda armatus* Keegan.—Only two species of this genus are known. *I. armatus* was described from *Thomomys bottae* in California and has also been found in *Dipodomys*, *Perognathus* and *Peromyscus* from California, New Mexico and Colorado. One specimen was collected from *T. bottae* in this study.

##### DERMANYSSIDAE

Dermanyssid mites are thought to be relatively specific and the family contains several species of medical and veterinary importance (Baker and Wharton, 1952).

*Hirstionyssus geomydis* (Keegan).—This genus is almost entirely restricted to rodents (Baker and Wharton, 1952), living in the host nest and attaching to the host only to feed. *H. geomydis* was common on *T. talpoides* and was also present on *T. bottae* and *G. bursarius*.

*Ornithonyssus* sp.—Members of this genus are true parasites of birds, mammals and reptiles. One specimen was found on *T. talpoides*.

##### PHYTOSEIDAE

Members of this family are frequently found on plants as predators of plant-feeding invertebrates. One unidentified specimen was found on *T. talpoides*.

*Garmania ponorum* (Ouds.).—Since members of this genus are non-parasitic, this mite would probably occur on small mammals by accident, or as a predator of other small arthropods. One specimen was found on *T. talpoides*.

##### LAELAPTIDAE

Laelaptid mites are common, relatively specific, ectoparasites of mammals.

*Haemolaelaps geomys* Strandtmann.—The genus *Haemolaelaps* occurs on birds and mammals and some species of the genus are apparently restricted to a single genus or family of mammals. *H. geomys* is found only on geomyids and occurs throughout the host range. This species was found on all four species of pocket gophers examined.

*Eulaelaps stabularis* (Koch).—This species was found on only two specimens of *T. talpoides*. It is associated with various small mammals in Europe and North America. Jameson (1950) found it commonly on *Blarina brevicauda* in California.

## IXODIDAE

*Ixodes sculptus* Neumann.—This tick is common on ground squirrels and their predators throughout the central and western United States and Canada (Gregson, 1956) and was the most common tick found in this study. Tryon (1947) found *Ixodes* sp. common on *T. talpoides* in Montana, but Howard and Childs (unpublished) found no ticks on *T. bottae* in California, even though a careful search was made for them. *I. sculptus* was especially common on *T. talpoides* in this study, but was also found on *T. bottae* and *G. bursarius*. Male *Ixodes* remain on the host only during mating, but females oviposit on the host for several weeks, or even months. No males were collected.

*Ixodes kingi* Bishop.—This tick is also a common parasite of ground squirrels and their predators in the prairies of the United States and Canada. It was found only on *T. bottae*.

*Dermacentor* sp.—A single, unidentifiable, larva was collected from *T. bottae*. Species of this genus are not separable at the larval stage, but the larva was either *D. parumapterus* or the Rocky Mountain wood tick, *D. andersoni*. These ticks feed on any of a wide range of hosts and often require a new host for each instar (Gregson, 1956).

## SARCOPTIDAE

Sarcoptid mites are skin parasites of warm-blooded animals. The family includes the scabies mite, *Sarcoptes scabiei*, and several other species responsible for sarcoptic mange. One unidentified sarcoptid was found on *T. talpoides*.

## LISTROPHORIDAE

Members of this family occur in the hair of small to medium-sized mammals. They apparently feed on sebaceous secretions (Trouessart, 1918). One female, probably *Mycophyes* sp., was found on a specimen of *G. bursarius*.

## LICE (MALLOPHAGA)

Since lice spend their entire life cycle on the host, they have been free to evolve a high degree of host specificity. Hopkins (1949) examined 50 species of wild mammals and found only six instances of the same trichodectid on two host species. In each case, closely allied species of the same genus of mammal were involved. This close association between lice and their hosts has also allowed the lice to evolve with their hosts, so that the origins of the host genera and families, and the history of their subsequent distributions, determine whether they are hosts to Anoplura or Mallophaga (Jellison, 1942). The Geomyidae are hosts to Mallophaga but not Anoplura.

## TRICHODECTIDAE

Trichodectid lice are common parasites of mammals and usually show a high degree of host-specificity (Hopkins, 1949).

*Geomydoecus californicus* (Chapman).—Hopkins (1949) lists *Thomomys bottae* as the true host of this species, although it has also been recorded from *Geomys arenarius* and *T. baileyi*. It seems to be a common parasite of *T. bottae* throughout its range in Colorado, and was also collected from *Geomys bursarius* in the vicinity of Colorado Springs and Canon City, where the ranges of *G. bursarius* and *T. bottae* meet.

*Geomydoecus chapini* Werneck.—The only previous record of this species is from a specimen of *Geomys personatus* from Tabasco, Mexico (Hopkins and Clay, 1952). On the basis of fresh specimens and museum skins examined during this study, this species appears to be generally distributed in Colorado as a parasite of *T. talpoides*. The northern limit of its range is not known. The

junior author examined a large series of museum skins of pocket gophers from Utah and *Geomydoecus chapini* was not found. This may be a species of Mexican origin which has followed the Rocky Mountain chain northward.

*Geomydoecus geomydis* (Osborn).—Hopkins (1949) lists *Geomys bursarius* as the true host of this species. There are several records of this louse from *Cratogeomys castanops* however, and it is the only louse known to occur on this genus of pocket gophers. *Geomydoecus geomydis* was not collected from *Geomys bursarius* during this study, but it occurred on all of the *Cratogeomys castanops* examined.

*Geomydoecus minor* Werneck.—Hopkins (1949) lists *Thomomys baileyi* as the host of *Geomydoecus minor*. It was common on the *T. bottae* specimens examined and seems to occur on this gopher throughout its range.

*Geomydoecus thomyus* (McGregor).—Hopkins (1949) lists *Thomomys talpoides* as the true host of this species, but it has also been recorded from *Thomomys bottae* and from *Thomomys monticola* in Oregon. This louse is widely distributed throughout the range of *T. talpoides* in the United States and Canada.

*Geomydoecus geomydis-californicus*.—*Geomys bursarius* is considered to be the true host of *Geomydoecus geomydis* and *Thomomys bottae* the true host of *Geomydoecus californicus* (Hopkins, 1949). None of the *Geomys bursarius* collected during this study were hosts of *Geomydoecus geomydis*, which occurred,

TABLE II.—Relative host specificities of ectoparasites of pocket gophers

	Primarily restricted to Geomyidae	General rodent parasites	Non-parasitic or accidental
MITES	<i>Hirstionyssus geomydis</i>	<i>Haemogamasus ambulans</i>	<i>Macrocheles</i> sp.
	<i>Haemolaelaps geomys</i>	<i>Ischryopoda armatus</i>	<i>Coprholaspis</i> sp.
		<i>Eulaelaps stabularis</i>	<i>Garmania panorum</i>
		<i>Ornithonyssus</i> sp.	
TICKS		<i>Ixodes sculptus</i>	
		<i>I. kingi</i>	
		<i>Dermacentor</i> sp.	
LICE	<i>Geomydoecus californicus</i>		
	<i>G. chapini</i>		
	<i>G. geomydis</i>		
	<i>G. minor</i>		
	<i>G. thomyus</i>		
FLEAS	<i>Foxella ignota</i>	<i>Thrassis petiolatus</i>	
	<i>Dactylopsylla percernis</i>		

instead, on *Cratogeomys castanops*. Specimens of *Geomys bursarius* collected in the vicinity of Colorado Springs and Canon City, near the range of *T. bottae*, were hosts to typical *Geomydoecus californicus*. Specimens collected north of these localities, along the front range of the Rocky Mountains, had lice which appeared to be intergrades between *Geomydoecus geomydis* and *Geomydoecus californicus*. These localities represent the western limit of the range of *Geomys bursarius*, and the lice that were collected probably represent a case of introgression.

#### FLEAS (SIPHONAPTERA)

##### CERATOPHYLLIDAE

*Foxella ignota* (Baker).—Fleas of this genus are true parasites of pocket gophers, although they also occur on pocket gopher predators and rodents which are closely associated with pocket gophers and use their abandoned burrows. *Foxella ignota* is widely distributed in the United States, Canada and Mexico, wherever pocket gophers occur, and has also been recorded from ground squirrels, weasels, burrowing owls, pocket mice, prairie dogs and deer mice (Hubbard, 1947). It occurred on all of the species examined in this study.

*Dactylopsylla percernis* Eads and Menzies.—Fleas of this genus, the "giant fleas of pocket gophers" (Hubbard, 1943), are restricted primarily to the Geomyidae. *D. percernis* was found only on *Cratogeomys castanops* during this study, but this species of flea is relatively rare and individuals generally occur singly or in pairs on the host (Hubbard, 1947). The range of the genus broadly overlaps that of *Foxella*, but *Dactylopsylla* populations are more scattered and less common.

*Thrassis petiolatus* (Baker).—One specimen was collected from *Thomomys bottae*. This flea is primarily associated with ground squirrels of the genus *Citellus* (Holland, 1949), but has also been collected from woodrats, marmots, cottontails and tree squirrels (Holland, 1949).

On the basis of the data in Table I and the foregoing accounts of the known associations of the ectoparasites collected, the relative host specificities of the ectoparasites are shown in Table II. Two mites, five lice and two fleas are primarily restricted to pocket gophers. Four mites, three ticks and a flea occur on pocket gophers but are known to be general rodent parasites. Three of the mites are considered to be non-parasitic and their occurrence on pocket gophers may have been accidental.

A close correlation was found between adult louse and flea population sizes and the body weights of their hosts, possibly indicating close host-parasite associations (Ward, 1957b). The product-moment correlation coefficients for these relationships are shown in Table III. The correlation coefficient  $r$  was computed as explained by Ward (1957b), using the formula:

$$r = \frac{\sum xy - \bar{x} \sum y}{\sqrt{(\sum x^2 - \bar{x} \sum x)(\sum y^2 - \bar{y} \sum y)}}$$

The higher correlation between lice and their hosts than between fleas and their hosts may be attributed to a closer parasitic relationship between the former.

TABLE III.—Product-moment correlations between host body weights and adult population sizes of lice and fleas

Host species	Mallophaga		Siphonaptera	
	n	r	n	r
<i>T. bottae</i>	22	0.78	22	0.69
<i>T. talpoides</i>	56	0.60	79	0.59
<i>G. bursarius</i>	12	0.77	12	0.57
<i>C. castanops</i>	6	0.95	6	0.76

## DISCUSSION

Various degrees of host-specificity are shown in the ectoparasite fauna of pocket gophers. None of the ectoparasites collected during this study is restricted throughout its range to a single host species, although four species of lice were confined to single hosts during this study. The flea, *Dactylopsylla percernis*, was only collected from *C. castanops*, but is known also from *T. talpoides* and *T. bottae* and the senior author has observed it on other species in Colorado. The fact that it was only recorded on *C. castanops* during this study is probably due to its general scarcity and the short period of time covered by the collections. Thus two mites, five lice and two fleas are primarily restricted to the Geomyidae, but none is restricted to a single species of pocket gopher.

Most of the general rodent parasites were relatively scarce on pocket gophers and occurred on only one or two host species. This was not the case, however, with the mite, *Haemogamasus ambulans*, or the tick, *Ixodes sculptus*. The genus *Haemogamasus* is restricted to burrowing rodents and insectivores, but little is known of the species *H. ambulans*. During this study it was abundant on *T. talpoides* and occurred also on *T. bottae* and *C. castanops*. *Ixodes sculptus*, a common parasite of ground squirrels, was relatively abundant on *T. bottae* and *T. talpoides* and was also found on *G. bursarius*. In view of their relative abundance on pocket gophers and their host associations during this study, both of these species should probably be considered as common ectoparasites of pocket gophers, even though not primarily restricted to pocket gophers.

Ectoparasite populations would appear to provide excellent material for an evaluation of the role of interspecific competition in animal communities. A fairly wide variety of species is available to the ectoparasite community, the environment is more or less uniform, and the necessary conditions for competition are often present. The evaluation of competition between species has largely been focused upon closely related species of the same genus which might tend to displace one another with respect to a particular ecological niche. Of the fourteen genera of ectoparasite recorded by Jameson (1950) from *Blarina brevicauda*, none was monotypic although six were represented locally by only one species. It was theoretically possible

for the remaining eight genera to have more than one species per genus parasitic on the short-tailed shrews of Jameson's study. However, Jameson (*op. cit.*) concluded that the species within a given family differ in occurrence or in habits, and that they compete on only a limited scale or not at all. In a study of the fleas parasitic on *Apodemus sylvaticus* and *Clethrionomys glareolus*, Evans and Freeman (1950) found as many as four species of flea on an individual host. *Ctenophthalmus agyrtes* and *Malaraeus penicilliger* occurred in sufficient numbers for their associations to be analyzed and were considered to be potential competitors. They showed a strong negative association on *Apodemus* and a moderate positive association on *Clethrionomys*. The authors concluded that the somewhat longer and coarser fur on *Clethrionomys* allowed these two species of flea to live side by side on that host and to avoid the direct competition that might occur on *Apodemus*. When two closely related species are found together on the same host it is often assumed, as in this study by Evans and Freeman (1950), that they occupy different niches and that competition is thus alleviated. Lice have been shown to occupy different ecological niches on birds (Hopkins, 1949; Ward, 1957b), but direct evidence for mammals is lacking. Multiple infestations of lice are common among hyraxes, for example, but it has not been shown that the different genera and species found on these animals prefer different parts of the body.

In the present study only ticks and lice were represented by more than one species of the same genus on a single host. The tick, *Ixodes kingi*, occurred with *I. sculptus* or not at all; although *I. sculptus*, the more abundant of the two, was frequently present when *I. kingi* was absent. There was no apparent tendency for the two species to exclude each other, nor was there any evidence that they occupied different parts of the host.

The lice *Geomydoecus thomyus* and *G. chapini* occurred together on 52.2 per cent of the 92 specimens of *Thomomys talpoides* examined. *G. californicus* and *G. minor* occurred together on 82.7 per cent of the 51 specimens of *T. bottae* examined. The fact that these ectoparasites were not mutually exclusive was also demonstrated by correlations between the numbers of each on a single host individual. The correlation between the numbers of *G. thomyus* and *G. chapini* on individual *T. talpoides* was 0.46 ( $P = .001$ ). The corresponding correlation for *G. californicus* and *G. minor* on *T. bottae* was 0.63 ( $P = .001$ ). If the members of these species pairs tended to exclude one another, one would expect negative correlations.

The data presented in this study are incomplete with respect to a number of important variables. They are based on collections in selected areas during only one season, and an extended study would show seasonal differences in abundance and distribution of the parasite species, would probably increase the list of ectoparasites known to occur on pocket gophers in Colorado, and might reduce the degree of host specificity shown locally by some species. The extent to which

these data apply to the question of interspecific competition, or lack of it, between closely related species would not be much affected however. There is no doubt that these species exhibit seasonal differences in abundance and have differences in habits—this much can be assumed, *a priori*, from the fact that they are different species. Nevertheless, when an opportunity for competition exists, there is no evidence to show that they exclude each other, or that they occupy niches which are different enough to preclude competition between them.

#### SUMMARY

A study was made of the ectoparasites of the four species of pocket gopher that occur in Colorado.

Of the ectoparasites collected, two mites, five lice and two fleas are primarily restricted to pocket gophers; four mites, three ticks and one flea are general rodent parasites; and three mites are non-parasitic and may have been accidentals.

Most of the general rodent parasites occurred in small numbers on only one or two host species; but the abundance and host associations of the mite, *Haemogamasus ambulans*, and the tick, *Ixodes sculptus*, suggest that they are common pocket gopher parasites.

Four species of lice were the only ectoparasites that were host-specific, although each of the lice has also been recorded from other hosts in other parts of its range.

There were two examples among the lice and one among the ticks of closely related species of the same genus occurring on the same host. The data showed that these species pairs were not mutually exclusive and there was no evidence that they occupied different ecological niches.

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# A Population Study of the Vole, *Microtus pennsylvanicus*

LOWELL L. GETZ

University of Michigan, Ann Arbor

Owing to the amount of time and effort required to live-trap small mammals, comparatively little is known concerning the population phenomena of even the more common species. One such species is the meadow vole, *Microtus pennsylvanicus*. Although several studies have been made of this rodent (Gunderson, 1950; Blair, 1948; Hamilton, 1940; Linduska, 1950), for the most part the investigators utilized snap-trapping data or based their results on live-trapping studies in which the intervals between trapping periods were longer than desirable, considering the rate of change of the various population factors. The short life span, as well as the rapid growth and development of *M. pennsylvanicus*, necessitates that samples of the population under study be taken at least at monthly intervals. Studies made at lesser intervals (or continuously) would permit following the population changes even more closely. Since trapping disturbs the population to a certain extent (death of animals in the traps and restriction of movements), intervals of less than one month may result in disturbances sufficient to offset the advantages gained by the closer inspection of the population. Consequently, an interval of approximately one month between trapping periods seems to be a suitable compromise.

The data presented in this paper were obtained during the course of a study of the ecology of *M. pennsylvanicus* in southern Michigan. Other phases of the study, being published separately, include an analysis of the factors influencing the local distribution of the species (Getz, in Press) and its home range, territoriality, and movement (in Preparation).

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## DESCRIPTION OF THE STUDY AREA

Two areas, an abandoned field ("old field") and a marsh, located in the University of Michigan's Mud Lake Research Area, Washtenaw County, Michigan, were studied. The areas were approximately 630 meters apart when measured by the most direct route (through unfavorable *M. pennsylvanicus* habitat), or 1020 meters apart when measured along a more favorable habitat. Although four individuals

moved from one area to the other during the course of the study, the individuals inhabiting each area are considered members of a separate population.

*Old field.*—This area is comprised of a field abandoned for approximately 15 years (confirmed by a local resident). In the northern part of the field is a small depression that contains a refuse heap; the heap is bordered by *Salix* sp., *Populus tremuloides*, and *Cornus racemosa*. The southern portion of the field slopes into a hardwood swamp. The soil is primarily sandy loam (Miami loam). Sheet erosion on the slopes has removed most of the top soil leaving a sandy clay.

The plant growth is relatively uniform over most of the field. The vegetation consists primarily of *Poa compressa*, *Potentilla intermedia*, *Daucus Carota*, and *Plantago lanceolata*. The surface is partly covered by a moss, *Brachythecium* sp. The eroded sites have a sparse cover while the low places support a more abundant growth.

A blue-grass pasture and a small grass-sedge marsh were near the old field. Both were favorable vole habitats and individuals undoubtedly were able to move back and forth between these sites and the field.

*Marsh.*—This area is for the most part a rather typical marsh. The dominant plants are sedges and grasses. One portion contains a considerable amount of *Solidago* sp. and *Aster* sp. In general the surface is low with the water table only a few centimeters beneath. During the wet season, water stands over most of the area. The soil throughout is typical of marshes (Dansereau, 1957); it contains much fibrous, peaty humus and a moderate amount of mineral matter. As indicated above, the soil moisture is high even when it is not inundated — being nearly saturated during the driest months. The sedges and grasses grow from small hummocks 5 to 10 centimeters in diameter. Each hummock rises 5 to 10 centimeters above the surface. The spaces between the hummocks are usually free of living vegetation. During the winter the dead vegetation falls over and forms a low canopy. Decaying vegetation also falls between the hummocks to form a tangled mat that covers the surface. In the summer the grasses and sedges completely cover the surface.

For more complete descriptions of the areas (including the species of plants present) as well as the adjoining habitats, see Getz (1959). The marsh is the more favorable *Microtus* habitat. The more abundant growth of grass-like vegetation (an average of 325 grams per square meter in the marsh compared with 65 in the old field), as well as the moist soil, results in a higher humidity and more moderate temperatures in the marsh than in the old field. Both of these conditions appear to be favorable for voles. Similarly the larger amount of vegetation in the marsh offers a greater available food supply as well as more protection from predators, especially hawks and owls.

## METHODS

The two areas were marked off in a grid pattern with a 12-meter interval. The entire old field was included in the study area while only that part of the marsh feasible to trap was included. The estimated area of each was 2.5 hectares for the old field and 3.6 hectares for the marsh. Where no natural boundaries occurred in the marsh, the study area was assumed to extend out one-half the average diameter of the home range of *M. pennsylvanicus* as determined from the trapping data, or 18 meters beyond the outer row of traps. The old field contained natural boundaries around almost the entire area. The marsh contained natural boundaries around two-thirds of the area.

A trapping period of five nights was employed throughout the study with the two areas being trapped once each month (for exact dates of trapping see Getz, *op. cit.*). Because of the size of the marsh study area (228 stations), two trapping periods were required to cover all stations (133 were trapped the first period). For the first four days of a period the traps were checked twice a day, once at 0800 to 1100 and again from 1600 to 1800 (the exact times depended on the time of sunrise and sunset). On the fifth day they were checked only in the morning; they were then picked up and moved in preparation for the next trapping period. The period of the study was September, 1957, through September, 1958.

Wooden multiple-catch traps of the type described by Burt (1940) were employed throughout the study. These proved effective with only a few voles escaping or chewing out. Bait consisted of equal amounts of sunflower seeds and commercial chicken scratch. No pre-baiting as such was employed. Traps normally were placed at the stations at least a day in advance of a trapping period. Since most of the traps contained some bait from the previous period, this may have served as a type of prebaiting. A small piece of cotton was provided in each trap from November through May to serve as insulation and to absorb moisture (urine, rain, or dew). Mortality in the traps was low. Of the 1,128 individuals captured a total of 6,412 times, only 74 (6.6%) died in the traps. Individuals were marked by toe clipping in a manner similar to that described by Gunderson (1950). No more than two toes were clipped on any one foot. No anesthesia was used. Only three instances of infection caused by the clipping were noted and one of these individuals was taken several months later. I do not believe that such clipping resulted in any appreciable mortality.

Some difficulty was experienced in the marsh where traps were disturbed by raccoons, opossums, weasels, and rabbits. Most of these animals had to be removed from the area by trapping if the study was to continue. Although the removal of the weasels (seven individuals) which were feeding on the voles (from examination of stomach contents) undoubtedly affected the population to some extent, no obvious effects were noted.

Field data (area, station number, species, individual number, sex, reproductive condition, and age class) were recorded on prepared forms. The capture data were transcribed onto 3 by 5 file cards (one for each individual).

#### POPULATION DENSITY

Densities of *M. pennsylvanicus* populations have been recorded by Hamilton (1940), Blair (1940), Bole (1939), and Townsend (1935). Depending upon the habitat and the method of sampling, these have varied from 0 to 92 per hectare. Hamilton (1940) has published data concerning population densities during various stages of the population cycle.

Population densities were computed for both areas based on the number of voles captured or known to be present each month. Some marked individuals not caught during one month but captured in subsequent months were considered to have been present during the months they were not captured.

The population density of the old field was at all times much less than that of the marsh (Fig. 1). At its highest point the population density of the old field was just equal to that of the marsh at its lowest point. This difference in density has been attributed to differences in the amount of graminoid vegetation present in each area (Getz, in press).

The marsh displayed greater monthly fluctuations in population density (extremes of 18 and 63 per hectare) than did the old field (6 to 18 per hectare). The more favorable conditions in the marsh allowed for a greater build-up in population sizes during the breeding seasons. The lesser vegetation cover in the old field resulted in more extreme temperatures and moisture conditions (Getz, *op. cit.*). This probably resulted in the movement of several individuals out of the old field

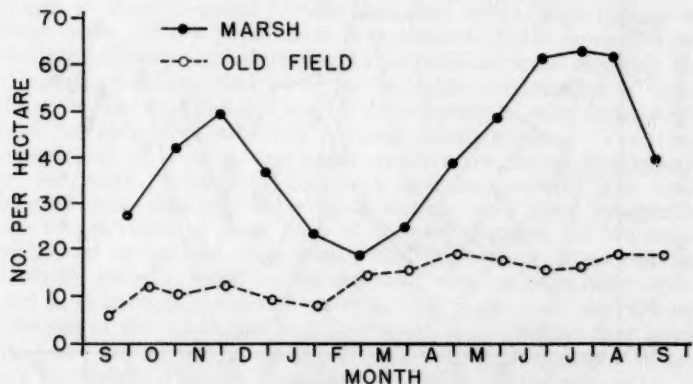


Fig. 1.—Population densities of *Microtus pennsylvanicus* in the two study areas.

and into nearby areas that supported more dense stands of vegetation. Trapping (during the July census) in a portion of the small marsh adjoining part of the old field resulted in the capture of one individual (out of seven captured) that had moved there from the old field. The lesser cover would also make the voles more susceptible to predation than in the marsh. Data concerning recaptures of individuals from month to month show that during the early summer and in the fall a greater percentage of the population was lost from the old field than from the marsh (Fig. 2). The peaks of the population, therefore, were suppressed somewhat in the old field so that the relative amount of fluctuation of population density was less than that of the marsh.

The data from the marsh indicate two definite peaks and two troughs of density during the year. Those from the old field indicate approximately the same characteristics although the peaks are somewhat smoothed and a drop in the density is not indicated by the September, 1958 data. The two peaks of population density result from the two main breeding seasons, spring and fall (see below). Breeding decreases during the summer resulting in a drop in the population density in the late summer or early fall. Owing to the relatively short life span of *M. pennsylvanicus*, few adult individuals survive from the spring to the fall breeding season. Also an increased loss of animals from the populations in late summer and during the winter (Fig. 2) further accentuates the depth of the troughs (especially in the marsh). From examination of the data, mortality, rather than movement, appears to be the major cause of loss of individuals.

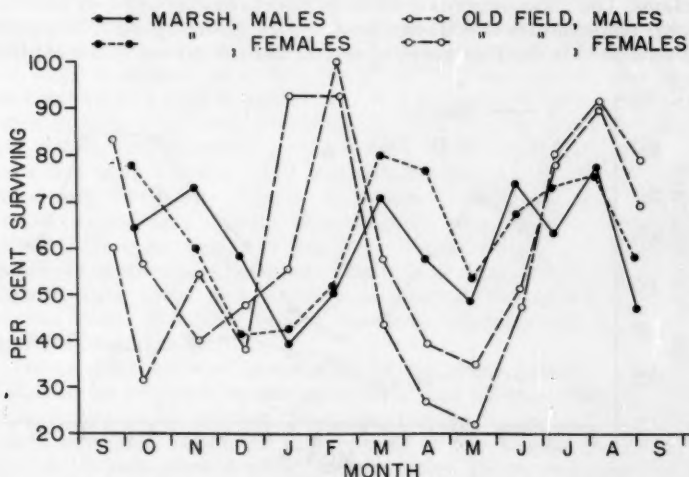


Fig. 2.—Percentage of the population present one month that survived until the next month.

In general the changes in population density in the old field were approximately 2 to 3 months ahead of those of the marsh. The earlier peak density in the old field in the spring results from an earlier breeding season in this area than in the marsh.

Since the study encompassed only one year, no evidence of a cycle was obtained. The population densities may have been slightly higher in September, 1958, than in September, 1957, but do not appear to be different enough to indicate an upward trend in the population levels. As stated above, the fluctuations in density that did occur were attributed to the limited periods of reproduction and are not indicative of a cyclic fluctuation.

#### SURVIVAL

Loss of individuals from a study area can occur in two ways, death of the individual or movement off the area. Blair (1948) stated that emigration accounted for only 10 per cent of the losses from a population. From data on movement of individuals this appears to be approximately true of the areas of the present study. Deaths can be caused by various factors, but losses to predators probably account for the vast majority of them (Blair, *op. cit.*).

Since data were obtained for a period of only one year, the information concerning survival of individuals is limited. It has been possible, however, to obtain a fairly clear indication of the length of survival in the two areas and to make comparisons. Two methods of determining survival were utilized. The first method was based on the estimated number of young produced by the population each month. The number of pregnant and lactating females observed each month was multiplied by the average number of offspring per litter. Hamilton (1941) and Bailey (1924) found the average number of young per litter of *M. pennsylvanicus* to be five. Counts of the number of young in the litters born in the traps and the number of embryos in those pregnant females that died in the traps indicate a similar mean for the populations here studied. Only those females definitely pregnant (and thus close to parturition) were recorded. It is assumed, therefore, that owing to the rapid development of voles (Hamilton, *op. cit.*; Bailey, *op. cit.*) the offspring of these individuals would be captured as subadults the next trapping period. Those individuals not yet weaned were not normally taken during that month and still were "subadults" the next trapping period. The subadults actually captured in a given month were then considered to be the survivors of those born of females pregnant the last trapping period or weaned since then. The percentages of survival in subsequent months, based on the estimated number born, were computed to determine a survival curve for *M. pennsylvanicus*. Owing to the age of the individuals and their small size, I believe that losses during the first month of life resulted primarily from deaths (especially to predators) rather than from movement off the area.

The second method recorded the length of time each individual remained on a study area after it was first captured. Thus, the per-

centage of those surviving each successive month was computed, based on the number captured for the first time a given month. In other words, of the individuals first captured in October, November, December, etc., the number surviving for each succeeding month was determined to obtain survival curves for each sex as well as for those first captured as adults or subadults.

Since there were relatively few captures of subadults (especially from the old field) the data from both areas and both sexes were combined to determine survivals from the estimated births. As can be seen (Fig. 3), mortality was far greater during the first month of life than at any other time. In both the marsh and the old field only 12 per cent of those estimated to have been born were actually captured. The semi-log plot shows that the curve of survival for the remaining months approaches a straight line, an indication of a constant specific rate of survival after the first month of life. The average life span of *M. pennsylvanicus* as indicated by this data is 0.7 months.

The high mortality rate most likely results from predation, probably by garter snakes. *Thamnophis sirtalis* and *T. sauritus* were both abundant in the area. Time was not available to make a food habit

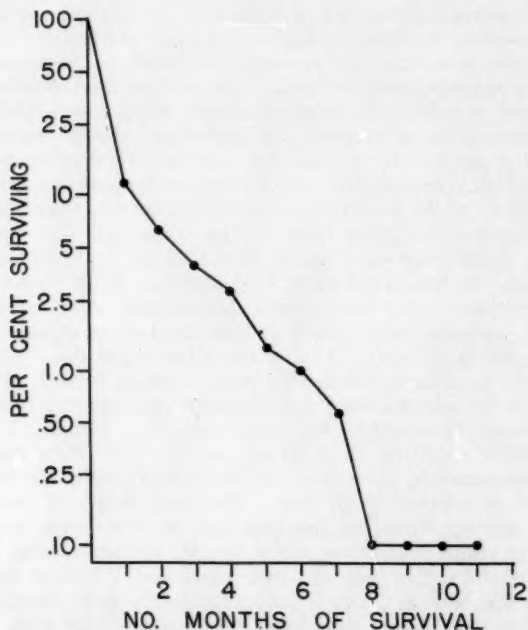


Fig. 3.—Semi-log plot of the survival curve from birth. Based on an estimated 1665 births.

TABLE I.—Mean survival of *Microtus pennsylvanicus* in the study areas (only those individuals first captured October, 1957, through March, 1958, are included)

Area	Sex	Age at first capture	No. of individuals	Mean survival (months)	sd
Marsh	Male	Adult	126	2.2	1.8
Marsh	Male	Subadult	21	2.7	2.0
Marsh	Female	Adult	133	2.1	1.8
Marsh	Female	Subadult	40	2.1	2.0
Old field	Male	Adult	49	1.6	1.1
Old field	Male	Subadult	21	1.9	1.7
Old field	Female	Adult	52	1.9	1.3
Old field	Female	Subadult	10	1.3	0.7

study of these species to confirm this assumption. Hamilton (1951) found that these snakes fed upon voles. Young voles, still in the nest, would be especially susceptible to predation by snakes.

No difference in the survival of either sex during the first month was found. Assuming the sex ratio to be equal at birth, the survival

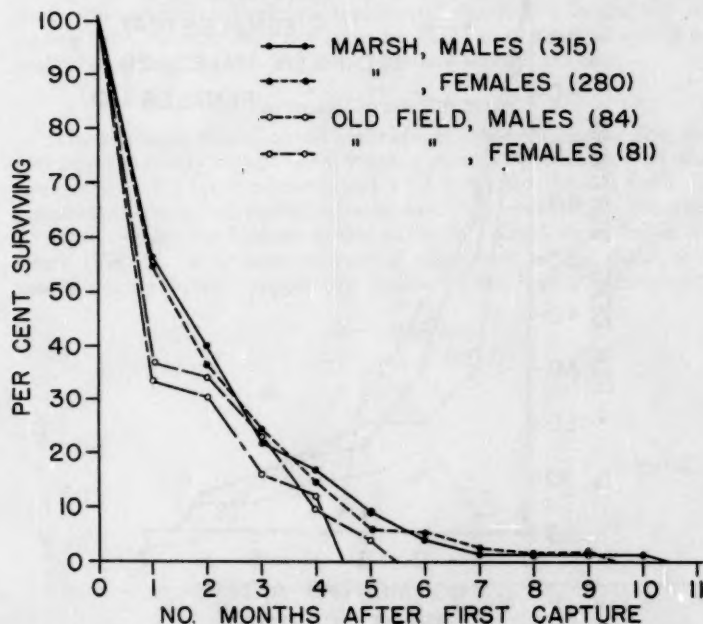


Fig. 4.—Survival of individuals first caught as adults. Figures in parentheses indicate the number of individuals involved.

of both sexes was approximately 12 per cent. The sex ratio of the individuals captured as subadults was 100 males to 101 females.

Figures 4 and 5 and Table I give the survival of individuals after their first capture. Blair (1948) found that the average time the individuals remained in his study areas was  $4.23 \pm .22$  months. My data indicate the time is approximately one half that recorded by him. Since his trapping periods were approximately three months apart, the resulting averages indicate most individuals to have been taken during only one trapping period. Blair's results, therefore, appear to be related more to the interval between trapping periods than to the actual survival of the voles on his study areas. The longest survival recorded in my study was 11 months (two individuals). Hamilton (1941) estimated the maximum longevity of *M. pennsylvanicus* under field conditions at 16 months.

The average survival (based on month of first capture) as well as the survival curves were similar for all the males and females in both areas (Fig. 4 and Table I). The data concerning those first captured as adults in the marsh, when plotted on a semi-log scale,

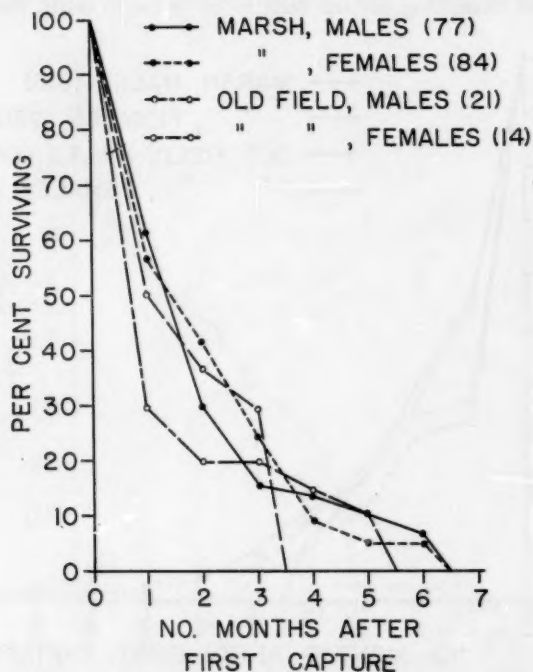


Fig. 5.—Survival of individuals first caught as subadults. Figures in parentheses indicate the number of individuals involved.

approach a straight line. This further indicates a constant specific survival of individuals after the first month of life. Data from the old field do not form a straight line, but fewer records were obtained and the data may not be significant. The survival of both sexes in the marsh was longer than, although not significantly different from, survival in the old field. As stated above, shorter survival time in the old field is attributed to the lesser amount of vegetation that resulted in less favorable moisture and temperature conditions as well as in greater predation.

Comparisons of the population losses between trapping periods in the marsh indicate a slightly greater loss during the winter months than at other seasons (Fig. 2). There is also a decrease in survival during the breeding season and another drop in August. The curves for the males and females show similar trends. The spring and summer data from the old field agree in general with those from the marsh. Those from the fall and winter differ somewhat, especially those for the December-January and January-February periods. The survival in the old field for both sexes during these latter periods is higher than at any other time during the year. Only a few individuals were present during these months and these data may not be significant. Owing to the harsh environmental conditions in the old field during the winter, it does not seem probable that survival would normally be as high as the few data obtained would indicate.

#### POPULATION STRUCTURE

The sex ratio based on all individuals captured during the study was approximately equal. The average monthly percentages of males were  $49.8 \pm 5.9$  for the marsh and  $49.9 \pm 8.1$  for the old field. The greatest percentage of males in the marsh (60) occurred in the month of March while the highest in the old field (70%) occurred in February (Fig. 6). A greater amount of movement of the males in the marsh during March apparently results in the higher percentage of

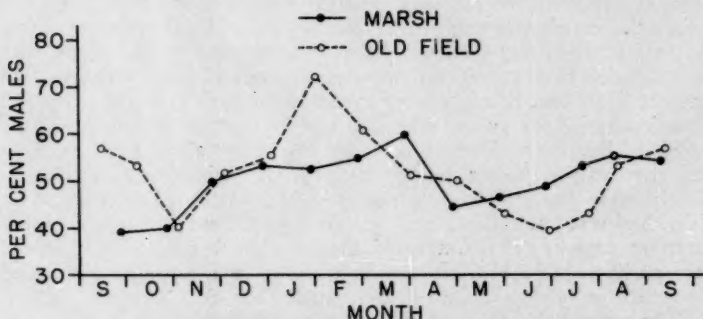


Fig. 6.—Monthly variation in the percentage of males (all age classes) in the population.

this sex in the population. The same appears to be true of the old field, but the number of individuals involved was not sufficient to determine this for certain.

Two age classes, subadult and adult, were distinguished by size and pelage. Because of two definite breeding seasons, the subadults made up an important part of the total population for only a portion of the year (Fig. 7). The difference in the breeding seasons in the old field and marsh resulted in differences in the percentage of subadults in the two areas for given months.

#### REPRODUCTION

The reproductive status of the adult females was determined by gentle palpation of the region of the uterus. Undoubtedly individuals in early stages of pregnancy were missed, but the limited time available for handling individuals did not permit a more thorough examination. In addition, a check was made of the vulva to see if it was open, an indication that the individual was in breeding condition.

Reproduction was limited primarily to two periods in both areas, spring and fall. This was reflected in the number of pregnant females and the appearance of young (Figs. 7 and 8). Gunderson (1950), in Minnesota, likewise found breeding to occur primarily in spring and fall. Extremely low temperatures in the winter and high temperatures in the summer probably result in unfavorable conditions for breeding. Hamilton (1941) has given evidence to support the relationship between temperature extremes and cessation of reproduction in *M. pennsylvanicus*. Temperature data for the two areas are given by Getz (in Press).

The breeding seasons in both areas are approximately the same except that in the old field the spring breeding commences earlier and ends earlier than in the marsh (Fig. 8). The spacing of the trapping periods in the two areas tends to overemphasize the later commencement of breeding in the marsh. The old field was trapped immediately after the marsh, but there was an interval of one week before the marsh was trapped again. Since the April trapping of the old field immediately followed the March trapping of the marsh, and no indication of any pregnant females was found in the marsh at that time, it is evident that breeding commenced earlier in the old field. Examination of the vulvae revealed none to be open in females in the marsh in February. Twenty per cent of the females in the old field had open vulvae during the March trapping (which occurred immediately after the February trapping of the marsh). A newly born individual was found dead in a path in the old field during the March trapping period. This further indicates that breeding commenced very early in this area. It is also obvious that breeding decreased sooner in the old field than in the marsh (Fig. 8).

The most plausible explanation for the earlier breeding in the old field is that the grass began growing earlier here than in the marsh. During the March trapping of the marsh, the surface was almost

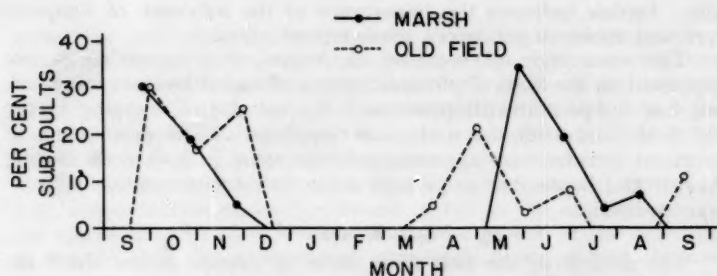


Fig. 7.—Monthly variation in the percentage of subadults in the two populations.

completely covered by ice and the vegetation had not begun to grow. The vegetation (particularly the grass) in the old field, on the other hand, had grown so that the green shoots were eight to ten centimeters tall by the time of the April trapping (immediately after the March trapping of the marsh). By the April trapping period in the marsh, the vegetation in this area had begun growing (25 to 30 centimeters tall) and reproduction of the voles was approaching its peak. Hoffman (1958) found that breeding in *Microtus californicus* and *M. montanus* is correlated with the growth of green vegetation.

The earlier decrease in breeding in the old field evidently is related to temperature and humidity conditions. Owing to the sparse cover in this area temperatures were rather high during the summer. Soil moisture became very low; probably air humidities were also low near the surface of the soil during these months. This contrasted with conditions in the marsh where the dense vegetation resulted in more moderate air temperatures and higher soil moistures (thus higher air humidity). That reproduction ceased completely in the old field while not ceasing entirely in the marsh (although dropping consider-

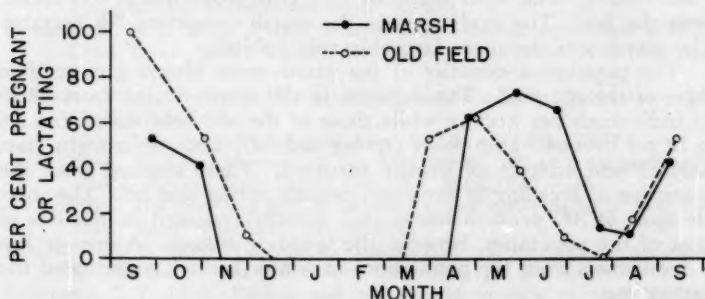


Fig. 8.—Monthly variation in the percentage of pregnant or lactating females in the two populations.

ably) further indicates the importance of the influence of temperature and moisture conditions upon reproduction.

The resumption of breeding in August and September is not explained on the basis of physical factors. Rainfall had not increased, nor had temperatures dropped until the last day of trapping in the old field (and after the study was completed). The percentages of pregnant females were approximately the same in both areas during August and September so perhaps some non-environmental "trigger" was involved.

#### CONCLUSIONS

The data from the two study areas in general follow the same trends. The differences that do occur, especially those concerning population densities, survival, and breeding apparently, result from the environmental differences in the two areas. The amount of cover with its modifying influence upon temperature and moisture conditions as well as protection from predators appears to control the time of occurrence of the various population phenomena.

As in many other species of small mammals, survival during the first month of life is very low for *M. pennsylvanicus*. After the first month there is no indication of senescence, that is to say, deaths occur at a constant rate regardless of the age of the animals. The survival data indicate that the approximate maximum age attained by *M. pennsylvanicus* in the wild is 11 to 12 months with an average of less than one month. Approximately 25 per cent of the adult individuals survive the three months between the spring and fall breeding seasons and only six per cent survive the five months between cessation of breeding in the fall and its resumption in the spring. *M. pennsylvanicus*, therefore, is essentially a semi-annual species in southern Michigan.

#### SUMMARY

Two populations of the vole, *Microtus pennsylvanicus* in southern Michigan were live-trapped at monthly intervals for 13 months. One population occurred in a 2.5 hectare abandoned field ("old field"). The other occurred in a grass-sedge marsh 630 meters from the first. The study area in the marsh comprised 3.6 hectares. The marsh was the more favorable vole habitat.

The population densities of the marsh were always greater than those of the old field. The densities in the marsh varied from 18 to 63 individuals per hectare while those of the old field varied from 6 to 18 per hectare. Two peaks (spring and fall) and two troughs (late summer and winter) of density occurred. These resulted from the restriction of breeding to two main periods, spring and fall. The short life span of *M. pennsylvanicus* (0.7 months) resulted in the loss of most of the population between the breeding seasons. A greater loss of individuals from the populations in winter further accentuated the fluctuations.

The greatest mortality occurred during the first month of life (88%). After that there is a constant specific rate of survival. The average length of time the adult individuals remained on the study

areas was approximately two months. The length of survival was somewhat less in the old field than in the marsh. This was attributed to the less favorable conditions of cover, food, moisture, and temperature in the old field that resulted in more emigration and/or a higher loss to predators. No significant difference was observed between the length of survival of males and females in either area.

Reproduction occurred primarily during two seasons, spring and fall. Reproduction began one month earlier in the old field than in the marsh, a result of an earlier start in the growth of the vegetation in the old field. Breeding almost completely ceased during the summer, resuming at approximately the same time (September) in both areas. The reason for the resumption of breeding in the fall did not appear to be correlated to any environmental factor.

Owing to the relatively short life span, *M. pennsylvanicus* is essentially a semi-annual species in southern Michigan.

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## An Ecological Study of Benthic Organisms in Three Illinois River Flood Plain Lakes

ANDREAS A. PALOUMPIS and WILLIAM C. STARRETT

*Illinois State Normal University and Illinois Natural History Survey*

This paper is concerned largely with the dynamics and changes in the benthic populations of three flood plain lakes located along the Illinois River near Havana, Illinois. For a number of years these lakes have been affected by sewage and industrial pollution from the Illinois River. Prior to 1926 Richardson (1921a,b; 1925a,b; and 1928) studied the bottom fauna of the Illinois River and certain of its flood plain lakes. Two of the lakes included in Richardson's work were studied during the present investigation.

Both the human population and industries along the Illinois River have nearly doubled since Richardson's (*op. cit.*) studies were made. In 1913-14 Richardson (1921a) found that benthic organisms in the river and lakes in the vicinity of Havana (Fig. 1) were those normally found in relatively clean waters. Between 1917 and 1920 there was an increase in pollution in the river which wiped out most of the former clean water species in the Havana area (Richardson, 1925b and 1928). By 1925 there had been only a mild improvement in sanitary conditions of the river. Improvements apparently have occurred in the sanitary conditions of the river since 1925. Sewage disposal plants built after 1925 in most urban areas along the river above Havana have helped to reduce pollution in the river. In the 1930's several large navigation dams were constructed on the river, and they have tended to reduce the rate of flow of the river, thereby, allowing more time for a natural breakdown of certain pollutants. However, pollution in the form of silt has greatly increased in the river and its flood plain lakes since the time Richardson made his investigations.

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## METHODS AND MATERIALS

The present study was started in July, 1952 and concluded in April, 1958. The bottom fauna samples were all taken in mud with a 6 x 6-inch Ekman dredge; dredgings were washed through a No. 30 sieve and the collected organisms preserved in formalin. Individual counts were made of the preserved organisms. For determining the numbers of Oligochaeta the anterior ends were counted. The few specimens of Crustaceans, Pelecypoda (other than Sphaeriidae), Corixidae, Nematoda, and Hydracarina taken in the collections were considered as accidental and were therefore excluded from the study. Wet weights of organisms were recorded to the nearest 0.01 gram. A sample of Sphaeriidae and Gastropoda weights with and without shells was made to determine a factor for calculating molluscan weights without shells. Shell weights were deducted from the molluscan weights by multiplying the wet weights of Sphaeriidae by 0.60 and of Gastropoda by 0.35. Weights of Trichoptera, Diptera and Oligochaeta were determined after the cases and/or mud were removed.

A total of 363 dredgings were made: 57 in Lake Matanzas, 130 in Quiver Lake, and 176 in Lake Chautauqua. Because of the relatively small number of samples taken, the samples for each sampling period from all stations in each lake were combined.

TABLE I.—Summary of chemical analyses of monthly water samples from Lake Matanzas, Lake Chautauqua and Quiver Lake, Illinois (June, 1953- May, 1954)

Symbols	Lake Matanzas			Lake Chautauqua			Quiver Lake		
	Range	Mean		Range	Mean		Range	Mean	
	(ppm or			(ppm or			(ppm or		
	pH units)			pH units)			pH units)		
pH	7.6-	8.6	8.3	7.8-	8.6	8.2	7.8-	8.4	8.0
Fe	0.4-	2.5	1.3	0.2-	7.6	1.8	0.3-	11.3	2.6
PO <sub>4</sub>	0.0-	0.5	0.2	0.1-	1.2	0.4	0.1-	1.0	0.4
SiO <sub>2</sub>	0.6-	17.7	7.1	0.7-	15.8	5.7	8.1-	17.0	12.7
CO <sub>2</sub>	1.0-	7.7	2.4	0.8-	9.0	3.0	2.0-	16.0	6.4
Cl	3.0-	13.0	7.9	7.0-	15.0	10.5	4.0-	15.0	8.9
SO <sub>4</sub>	40.3-	76.7	51.4	50.4-	93.4	68.8	39.1-	91.3	60.8
NO <sub>3</sub>	0.0-	4.5	2.1	0.0-	4.1	1.1	2.3-	10.4	6.4
NH <sub>4</sub>	0.3-	0.7	0.4	0.1-	0.5	0.3	0.0-	0.5	0.2
Ca	36.5-	53.5	45.2	43.6-	57.0	49.2	55.3-	76.0	62.6
Mg	14.6-	20.0	17.2	16.9-	24.4	21.1	19.1-	26.2	20.6
Na	1.8-	12.0	7.9	4.1-	12.2	8.5	1.4-	14.6	8.4
Alkalinity (as CaCO <sub>3</sub> )	96.0-164.0	135.3		124.0-160.0	141.7		148.0-220.0	186.0	
Hardness (as CaCO <sub>3</sub> )	157.0-216.0	183.8		179.0-243.0	209.8		217.0-298.0	248.3	

Representative organisms from various dredgings were submitted to specialists for identification. The remainder of the identifications were made by us on the basis of the determinations of the specialists.

Test netting for black crappies, *Pomoxis nigromaculatus*, was done with 1-inch wing nets (with leads) as described by Starrett and McNeil (1952) and Starrett and Barnickol (1955).

Water samples were collected at monthly intervals between June, 1953 and May, 1954 from each lake. The water samples were delivered within 24 hours to the Water Survey Division Laboratory at Champaign, Illinois, for chemical determinations. The pH of each water sample was determined in the field.

Results of chemical analyses are summarized in Table I. Chemical characteristics for the three lakes were quite similar, except that car-



Fig. 1.—Map showing the Illinois River and locations of Lake Chautauqua, Quiver Lake and Lake Matanzas, Illinois.

bon dioxide, calcium, alkalinity and hardness were slightly higher in Quiver Lake than in the other two lakes. The analyses indicated that all three lakes were rich in nutrients.

A total of 24 water samples for bacteriological analysis was taken during 4 collecting periods from each lake between August and December, 1953. Lake levels remained low during this period. Samples were taken from both the surface and near the bottom of the lakes. They were iced immediately and delivered within two hours for analysis to the Division of Laboratories of the Illinois Department of Public Health at Springfield, Illinois. The analyses are discussed later in this paper. MPN refers to the most probable number of organisms per 100 ml (Hoskins, 1934).

#### DESCRIPTIONS OF LAKES AND SAMPLING STATIONS

The three lakes studied in this investigation are located in Mason County, Illinois, (Fig. 1) in the flood plain of the Illinois River, and are flooded periodically by the river. Most of the lake bottoms are covered with a layer of loose sediment, mainly deposited since the early 1930's from silt-laden flood waters. The lakes all have narrow-sandy beaches along their bluff-side shores. Seepage of effluents from septic tanks and privies at cottage sites along the bluffs overlooking the lakes provide a source of minor pollution in the lakes.

#### LAKE MATANZAS

Lake Matanzas covers about 347 acres at normal summer water levels and is 8.5 to 9.0 feet deep. During low river stages the lake is separated from the river by a low head dam and natural river em-

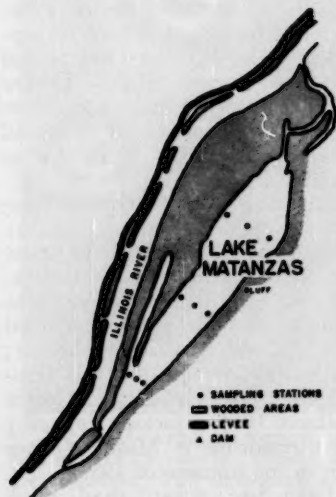


Fig. 2.—Map of Lake Matanzas, Illinois, showing the nine sampling stations used in the study and the site of the lake with reference to the Illinois River.

bankments (Fig. 2). The water level of the lake is raised once or twice a year by flood waters of the Illinois River. Submergent aquatic vegetation was absent from the lake; however, vegetation formerly flourished in the lake (Richardson, 1921a). The effects of turbidity upon aquatic vegetation in an Illinois River flood plain lake have been discussed by Jackson and Starrett (1959).

The abundant fishes in Lake Matanzas are: bluegill (*Lepomis macrochirus*), black crappie, white crappie (*Pomoxis annularis*), gizzard shad (*Dorosoma cepedianum*), bigmouth buffalo (*Ictiobus cyprinellus*), carp (*Cyprinus carpio*), and spottail shiner (*Notropis hudsonius*).

At Lake Matanzas the bacterial coliform counts ranged from  $<23$  to 620 MPN/100 ml and the enterococcus counts ranged from  $<2.3$  to 130 MPN/100 ml.

The nine sampling stations in Lake Matanzas were located on three transects as indicated in Figure 2. The bottom fauna samples were taken at the various depths and seasons given in Table II. Most of the samples at Lake Matanzas were taken during the month of October.

#### QUIVER LAKE

Quiver Lake differed from the other two lakes in that it was connected at all times with the Illinois River (Figs. 3 and 4). At low river stages, the river flows only through the extreme lower end of the lake, but at a river stage of about 8.0 feet at Havana (14.0 ft. flood stage) a portion of the river flows through the entire lake. Current was seldom perceptible in Lake Matanzas or Lake Chautauqua, even during periods of high river stages.

Quiver Lake covers about 408 acres at normal summer water levels. For purposes of this study, Quiver Lake was arbitrarily separated into three areas (Fig. 4). Most of Upper Quiver Lake tended to become dry during periods of low river stages; Middle Quiver Lake did not have a current present when the river stage was below 8.0 feet; and Lower Quiver Lake was actually a part of the river and some current was always present. Benthic studies of Quiver Lake were conducted primarily on Middle Quiver Lake.

At low river stages the maximum depth of Middle Quiver Lake was 6.5 to 7.0 feet. In 1914 and 1915 when Richardson (1921a) studied Quiver Lake the maximum depth was 12.0 feet at low water stages. Much of the lake has silted-in since the time of Richardson, and in the 1920's more water was diverted from Lake Michigan into the river than at present. Formerly, higher aquatic plants abounded in Quiver Lake (Hart, 1895; Kofoid, 1903; and Richardson, 1921a); whereas, at the time of the present investigation vegetation was completely absent from the lake. In 1953 and 1954, turbidity in Quiver Lake ranged from 25 to 775 ppm. (Jackson, 1954). Jackson (*op. cit.*) detected the presence of a temporary thermocline in Middle Quiver Lake during a period of warm weather in the summer of 1953.

The abundant fishes in Quiver Lake are: gizzard shad, black

crappie, bullheads (*Ictalurus* spp.), bigmouth buffalo, carp, and emerald shiner (*Notropis atherinoides*).

The coliform counts from Middle Quiver Lake in 1953 ranged from 230 to 24,000 MPN/100 ml and the enterococcus counts ranged from <2.3 to 620 MPN/100 ml.

Six sampling stations located on two transects were used on Middle Quiver Lake (Fig. 4). On Upper Quiver Lake three sampling stations were used, and on Lower Quiver Lake four sampling stations



Fig. 3.—An aerial photograph, taken in 1954, of Quiver Lake and the lower part of Lake Chautauqua, Illinois. During a period of high water the two lakes are connected. The photograph depicts the relationship between the Illinois River and Quiver Lake at a moderately high river stage.

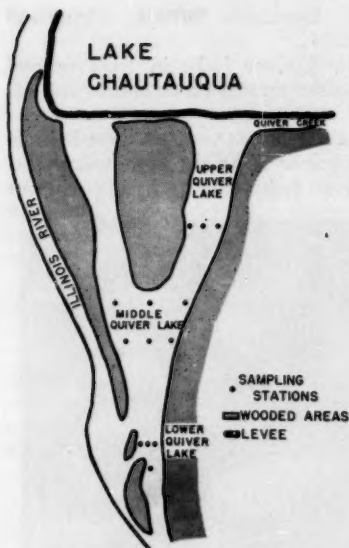


Fig. 4.—Map of Quiver Lake, Illinois, showing the sampling stations used during the investigation. Quiver Creek shown on the map flows directly into the river at low river stages.

were used (Fig. 4). The water depths at the time dredgings were made are given in Table III.

#### LAKE CHAUTAUQUA

At normal lake stage (435.0 ft. mean sea level) Lake Chautauqua covers 3,562 acres. The lake is a part of the Chautauqua National Wildlife Refuge and is managed primarily for waterfowl by the U. S. Fish and Wildlife Service. A system of levees with spillways and control gates separate the lake from the Illinois River at normal river stages (Fig. 5). At a river stage of about 12.2 feet at Havana the river enters the lake and this usually occurs once or twice a year.

Most of Lake Chautauqua is between 2 and 3 feet deep at normal lake level and at such a level nearly the entire lake is within the euphotic zone (Jackson and Starrett, 1959). No period of summer stagnation has been known to occur in the lake. Sago pondweed (*Potamogeton pectinatus*) becomes abundant in years when water levels remain low and stable during the growing season. During this investigation pondweed was abundant only in 1953 and 1956. Stall and Melsted (1951) found in 1950 that within a 23.8-year period the storage capacity of Lake Chautauqua had been reduced 18.3 percent by sedimentation. Turbidity of the lake between 1953 and 1956 varied from <25 to 800 ppm (Jackson and Starrett, 1959).

The most abundant fishes in Lake Chautauqua are: gizzard shad, white crappie, black crappie, bluegill, freshwater drum (*Aplodinotus grunniens*), bigmouth buffalo, carp, yellow bass (*Roccus mississippien-*

sis), channel catfish (*Ictalurus punctatus*), emerald shiner, and spot-tail shiner.

Coliform counts at Lake Chautauqua ranged from <23 to 2,400 MPN/100 ml, and enterococcus counts ranged from <2.3 to 6,200 MPN/100 ml.

On Lake Chautauqua benthic samples were taken at 21 sampling stations located on 7 transects established by Stall and Melsted (1951) (Fig. 5). The water depths at which the dredgings were made are summarized in Table IV.

#### BOTTOM FAUNA

The bottom fauna data presented here are given as standing crops per square foot. No attempt was made to determine the production of benthic organisms in the manner described by Lundbeck (1926), in which he estimated that the annual production in the Plöner See was about three or four times the average summer fauna. The studies of Hayne and Ball (1956) in Michigan indicated that in the presence of fish the average production of bottom fauna fish food during the growing season was about 17 times that of the standing crop. The standing crops given in the present paper are therefore merely only a fraction of the actual production that probably occurred each year in the lakes studied.

The benthic population differed considerably among the three lakes, particularly on a weight basis (Fig. 6 and Table V). The weight of bottom fauna of Middle Quiver Lake was comprised largely of



Fig. 5.—Map of Lake Chautauqua, Illinois, showing the relationship of the lake to the Illinois River. The map also shows the locations of the 21 sampling stations used during the study.

mollusca; whereas, in Lake Chautauqua insect larvae predominated. Worms and insect larvae were the important constituents of the bottom fauna in Lake Matanzas. In Lake Chautauqua and Lake Matanzas, mollusca formed only a small part of the total population. On

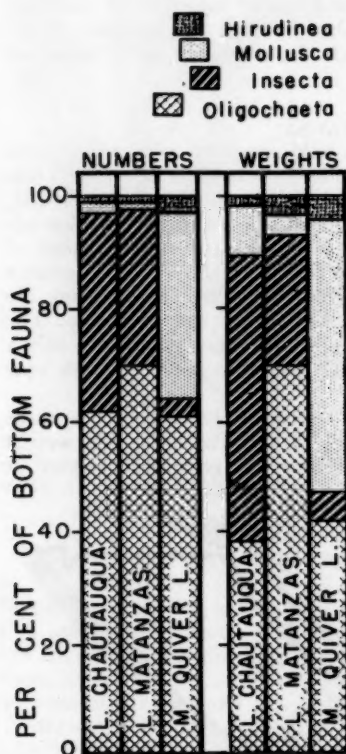


Fig. 6.—Composition of bottom fauna organisms at Lake Chautauqua (1952-56), Lake Matanzas (1952-56) and Middle Quiver Lake (1952-58), Illinois.

TABLE II.—Depths in feet at which bottom fauna samples were taken at Lake Matanzas, Illinois, 1952-56

Season		Range in depth	Mean depth
1952	Fall	1.8- 4.5	3.1
1953	Spring	6.6-10.6	8.8
1953	Summer	3.3- 7.2	5.7
1954	Fall	3.5- 8.5	6.3
1955	Fall	3.5- 8.5	6.3
1956	Fall	3.5- 8.0	6.0

a basis of numbers, worms formed more than 60 per cent of the total benthic organisms collected from all three lakes (Fig. 6).

The average annual standing crops as determined for each lake varied considerably from year to year (Fig. 7). The high standing crop of 14 grams per square foot (excluding shell weights) in 1952 in Middle Quiver Lake was comprised largely of snails and fingernail clams. The standing crop of mollusca in that lake dropped from 10.1 grams in 1952 to 1.4 grams in 1953. Other than in 1953 the standing crop of organisms at Lake Matanzas remained approximately the same each year. In most years the standing crop of benthic organisms in Lake Chautauqua was nearly double that of Lake Matanzas. The chief difference between those two lakes was in the greater abundance of dipterous larvae that occurred in Lake Chautauqua (Fig. 7).

TABLE III.—Depths in feet at which bottom samples were taken at Quiver Lake, Illinois, 1952-58

Year and name of lake	Range in depth	Mean depth
Upper Quiver Lake		
1952	0.4- 4.1	2.9
1953	1.1- 8.5	5.2
1957	6.0- 9.5	7.9
Middle Quiver Lake		
1952	0.7- 8.9	4.1
1953	1.0-13.3	5.3
1954	1.0-12.5	6.0
1955	3.0- 9.0	4.7
1956	6.5-12.0	8.9
1957	7.5-13.0	9.8
1958	9.0-14.5	11.4
Lower Quiver Lake		
1952	1.3-11.0	6.0
1953	2.0-13.5	7.7
1954	3.5-10.0	6.6

TABLE IV.—Depths in feet at which bottom fauna samples were taken at Lake Chautauqua, Illinois, 1952-56

Season	Range in depth	Mean depth
1952 Summer	1.4-3.8	2.8
1952 Fall	1.4-3.8	2.6
1953 Spring	2.5-5.5	4.2
1953 Summer	1.1-4.1	2.7
1954 Summer	1.5-3.5	2.4
1955 Summer	1.0-3.5	2.1
1956 Summer	1.7-5.1	3.1

The various invertebrate organisms identified from the three lakes are listed below. The classification of Tendipedini used by Townes (1945) was followed in this paper. After each organism listed below is the lake or lakes in which it was collected, with the lakes being designated as: (M) for Lake Matanzas, (Q) for Quiver Lake, and (C) for Lake Chautauqua.

## ANNELIDA

## OLIGOCHAETA

- Limnodrilus* spp. (M, Q, & C)      *Dero* sp. (M, Q, & C)  
*Tubifex* sp. (M, Q, & C)

## HIRUDINEA

- Helobdella stagnalis* (Linn.)      *Placobdella montifera* (Moore)  
 (M, Q, & C)      (M & Q)  
*H. elongata* (Castle) (M, Q, & C)      *Myzobdella moorei* (Meyer)  
*H. lineata* (Verrill) (Q)      (Q & C)  
*Erpobdella punctata* (Leidy)      *Actinobdella inequiannulata*  
 (M & Q)      (Moore) (C)  
*Glossiphonia complanata* (Linn.)      *Dina* sp. (Q)  
 (Q)

## ARTHROPODA

## INSECTA

## EPHEMEROPTERA

- Hexagenia limbata* (Serv.) (Q)      *Caenis* sp. (C)  
*Hexagenia* sp. (M)

## ODONATA

- Anax* sp. (Q)      *Enallagma signatum* (Hagen) (C)

- Ischnura* sp. (C)

## MEGALOPTERA

- Sialis* sp. (Q & C)      *Chauliodes* sp. (Q)

## TRICHOPTERA

- Oecetis inconspicua* (Walker)  
 (Q & C)

## COLEOPTERA

- Stenelmis* sp. (Q)

## DIPTERA

- Chaoborus punctipennis* (Say)      *Hydrobaenus* sp. (Q)  
 (M, Q, & C)      *Tendipedini* (tribe) (C)  
*Pentaneura* (*Monilis* sp.) sp. (Q)      *Polypedilum* sp. (M)  
*Pentaneura* nr. *decolorata* (Mall.)      *Cryptochironomus digitatus* (Mall.)  
 (Q & C)      (M, Q, & C)  
*Anatopynia* sp. (C)      *C. nr. digitatus* (Mall.)  
*Pelopia* sp. (M, Q, & C)      (M, Q, & C)  
*P. nr. stellata* (Coq.) (Q)      *C. sp. (fulvus* (Joh.) ? ) (C)  
*P. sp. B.* (Joh.) (C)      *Tendipes* sp. (M, Q, & C)  
*Procladius* sp. (M, Q, & C)      *T. plumosus* (Linn.) (M & C)  
*P. nr. bellus* Loew (C)      *T. nr. plumosus* (Linn.)  
*P. nr. choreus* Meigen (C)      (M, Q, & C)  
*P. choreus* Meigen (C)      *T. staegeri* (Lund.) (C)  
*Coelotanytus concinnus* (Coq.)      *Glyptotendipes* sp. (C)  
 (M, Q, & C)      *G. sp. prob. labiferus* (Say) (C)  
*C. nr. concinnus* (Coq.) (C)      *Palpomyia* sp. (M, Q, & C)  
*Cricotopus* nr. *fugax* (Joh.) (C)      *P. nr. tibialis* (Meigen) (M & C)

## MOLLUSCA

## GASTROPODA

<i>Valvata tricarinata</i> (Say) (Q & C)	<i>C. integrum</i> (Say) (Q)
<i>V. lewisi</i> (Cur.) (Q)	<i>C. rufum</i> (Hald.) (Q)
<i>Viviparus contectoides</i> (Bin.) (Q)	<i>Amnicola limosa</i> (Say) (Q)
<i>V. intertextus illinoisensis</i> (Baker) (Q)	<i>Cincinnatia emarginata</i> (Küst.) (Q)
<i>Lioplax subcarinata</i> (Say) (Q)	<i>Pleurocera acuta</i> Raf. (Q)
<i>Campeloma decisum</i> (Say) (Q)	

## SPHAERIIDAE

<i>Sphaerium</i> sp. (M, Q, & C)	<i>Pisidium</i> sp. (M, Q, & C)
<i>Musculium</i> sp. (M, Q, & C)	

In the following sections the abundance and ecological relationships of the various organisms are discussed. The groupings used do not necessarily follow the usual phylogenetic order but have been so arranged to facilitate presentation of the material in a coherent manner.

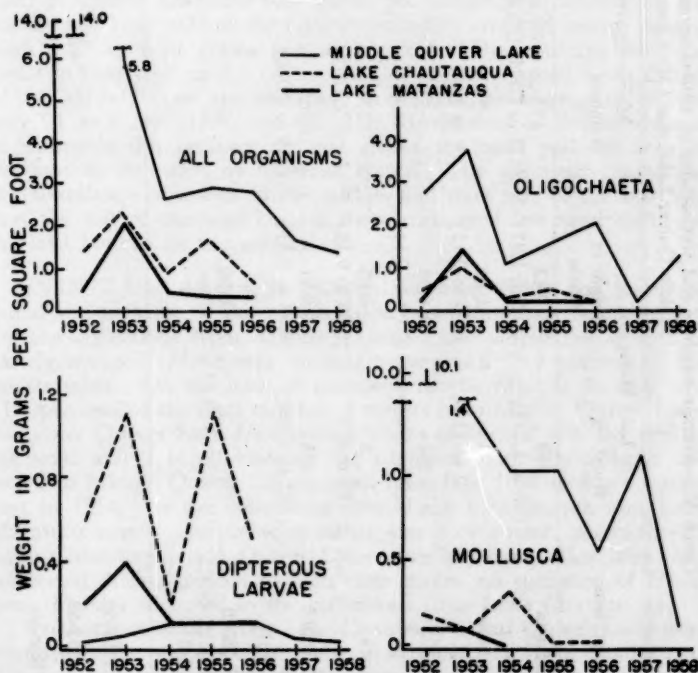


Fig. 7.—Annual fluctuations of standing crops of various benthic organisms at Lake Chautauqua, Lake Matanzas and Middle Quiver Lake, Illinois.

TABLE V.—Average numbers and wet weights of bottom organisms per square foot at Lake Matanzas,  
Middle Quiver Lake, and Lake Chautauqua, Illinois

Organisms	Lake Matanzas <sup>1</sup>		Middle Quiver Lake <sup>2</sup>		Lake Chautauqua <sup>1</sup>	
	Numbers	Weight in grams	Numbers	Weight in grams	Numbers	Weight in grams
Oligochaeta	348 (86 to 1,223) <sup>3</sup>	0.62 (0.17 to 1.97)	675 (171 to 1,524)	1.87 (0.34 to 3.83)	547 (129 to 1,303)	0.58 (0.17 to 1.09)
Hirundinea	1 (0 to 7)	0.03 (0.00 to 0.15)	25 (0 to 134)	0.18 (0.00 to 0.84)	4 (0 to 7)	0.02 (0.00 to 0.05)
Insecta	138 (79 to 310)	0.21 (0.09 to 0.54)	33 (4 to 61)	0.22 (0.01 to 0.46)	316 (160 to 528)	0.76 (0.26 to 1.49)
Mollusca	8 (0 to 20)	0.05 (0.00 to 0.15)	375 (2 to 2,410)	4.79 (0.19 to 20.77)	19 (0 to 41)	0.23 (0.00 to 0.52)
Total (Shell weight included)	495 (182 to 1,560)	0.91 (0.26 to 2.81)	1,108 (249 to 4,086)	7.06 (1.44 to 24.71)	886 (350 to 1,670)	1.59 (0.63 to 2.69)
Total (Shell weight excluded)	—	0.90	—	4.44	—	1.50

<sup>1</sup> 1952-56.

<sup>2</sup> 1952-58.

<sup>3</sup> Range.

**OLIGOCHAETA:**—Most of the worms taken in the benthic collections from all three lakes were species of the genus *Limnodrilus*. The abundance of worms (largely Tubificidae) (Table V) in the lakes probably reflected the richness of organic substances found in the lake bottoms. Soil analyses made from samples collected from the bottom of Lake Chautauqua indicated that the sediment deposits from that lake were quite high in fertility (Stall and Melsted, 1951). Soil analyses were not available for the other two lakes studied.

The abundance of worms in the lakes varied from year to year (Fig. 7). In 1953 worms were more abundant in all three lakes than in any other year of the study. Water levels were low in 1953 and such conditions possibly favored the development of large worm populations. Again in 1956 water levels were low, and the worm population in Middle Quiver Lake was higher than for any other time between 1954 and 1958, although in Lake Chautauqua and Lake Matanzas worm populations did not increase in size in 1956 (Fig. 7).

In 1953 the standing crop of worms on the cottage side (bluff side) of Quiver Lake was 0.04 grams per square foot, whereas in the middle and river side of the lake the standing crops of worms ranged from 5.27 to 6.19 grams per square foot. The coliform bacterial count in that year on the cottage side of the lake varied from 230 to 24,000 MPN/100 ml and elsewhere in the lake the count ranged from only 94 to 6,200 MPN/100 ml. The distribution in the abundance of worms in this instance did not reflect the most polluted area of the lake as indicated by bacterial counts. The apparent reason for the abundance of worms in the middle and river side of the lake was that the soil of the lake bottom there contained less sand than did the lake bottom on the cottage side.

**INSECTA:**—All insects collected were in either the larval or pupal stage. Most of the insects taken were dipterous larvae except for the collections from Middle Quiver Lake where the weight of mayfly nymphs (*Hexagenia limbata*) comprised 75.4 percent of the insects taken. On the basis of numbers, mayfly nymphs formed only 11.8 per cent of the total number of insects from Middle Quiver Lake. In Lower Quiver Lake *Hexagenia limbata* comprised 43.0 per cent of the total weight of all insects. The numbers of mayfly nymphs collected in Middle Quiver Lake ranged from 0 in 1958 to 8 per square foot in 1954. In the collections from Lake Chautauqua and Lake Matanzas mayfly nymphs were either scarce or absent. Even though Lake Chautauqua and Quiver Lake were adjoining lakes and were connected during periods of high river stages, no specimen of *Hexagenia limbata* occurred in the collections from Lake Chautauqua.

Trichoptera larvae from Lake Chautauqua and Quiver Lake were confined to the one species, *Oecetis inconspicua*. In Lake Chautauqua the single species of Trichoptera comprised 0.3 per cent of the total number of insects taken in the benthic collections which on a weight basis amounted to 2.0 per cent of the total weight of insects. Trichop-

tera larvae formed less than 1.0 per cent of the total number and weight of insects taken from Middle Quiver Lake. No Trichoptera larva appeared in the collections from Lake Matanzas.

Odonata, Coleoptera and Megaloptera larvae were scarce in the benthic collections from all three lakes and formed only a small, minor part of the insect fauna. Damselfly nymphs, however, did occur abundantly on sago pondweed plants in Lake Chautauqua.

A summary is given in Table VI of the dipterous larvae collected in the bottom samples of these lakes. *Chaoborus* sp. was the most common dipterous larva taken at Lake Matanzas. This form was quite scarce in the collections from the other lakes. The scarcity of *Chaoborus* in Lake Chautauqua may have been related to the shallowness of that lake as compared with the greater depths present at Lake Matanzas (Tables II & IV). Cronk (1932) working in Ontario found that *Chaoborus* did not occur in depths of less than 20 feet, and that large lakes were not suitable for the genus.

Dipterous larvae of the genera *Pelopia*, *Procladius* and *Coelotany-*

TABLE VI.—Kinds, average numbers and wet weights of dipterous larvae per square foot at Lake Matanzas, Middle Quiver Lake and Lake Chautauqua, Illinois

Kinds	Lake Matanzas <sup>1</sup>		Quiver Lake <sup>2</sup>		Lake Chautauqua <sup>1</sup>	
	No.	Per-cent	No.	Per-cent	No.	Per-cent
<i>Chaoborus</i> sp.	38	27.5	*	—	*	—
<i>Pentaneura</i> sp.	0	—	1	3.6	1	0.3
<i>Anatopynia</i> sp.	0	—	0	—	*	—
<i>Pelopia</i> sp.	31	22.5	7	25.0	121	38.9
<i>Procladius</i> sp.	22	15.9	8	28.5	93	29.9
<i>Coelotanytus</i> sp.	17	12.3	8	28.5	40	12.9
<i>Cricotopus</i> sp.	0	—	0	—	*	—
<i>Hydrobaenus</i> sp.	0	—	*	—	0	—
<i>Tendipedini</i> (Tribe)	0	—	0	—	5	1.6
<i>Polypedilum</i> sp.	*	—	0	—	0	—
<i>Cryptochironomus</i> sp.	1	0.7	1	3.6	4	1.3
<i>Tendipes</i> spp.	3	2.2	1	3.6	23	7.4
<i>Glyptotendipes</i> sp.	0	—	0	—	*	—
<i>Palpomyia</i> sp.	22	16.0	1	3.6	21	6.7
Undetermined	4	2.9	1	3.6	3	1.0
Total	138	100.0	28	100.0	311	100.0
Weight in Grams	0.21	—	0.05	—	0.73	—

<sup>1</sup> 1952-56.

<sup>2</sup> 1952-58.

\* Denotes less than 0.5 organism per square foot.

*pus* were common in the collections from all three lakes. At Lake Chautauqua *Tendipes* spp. varied from 1 to 61 organisms per square foot during the 1952-56 period and formed an important part of the dipterous weight from that lake.

We believe that the scarcity of dipterous larvae in Quiver Lake was related to the abundance of snails and other mollusca that occurred in that lake (Fig. 6). The effects snails have upon dipterous larvae and other organisms were discussed in some detail by Richard-

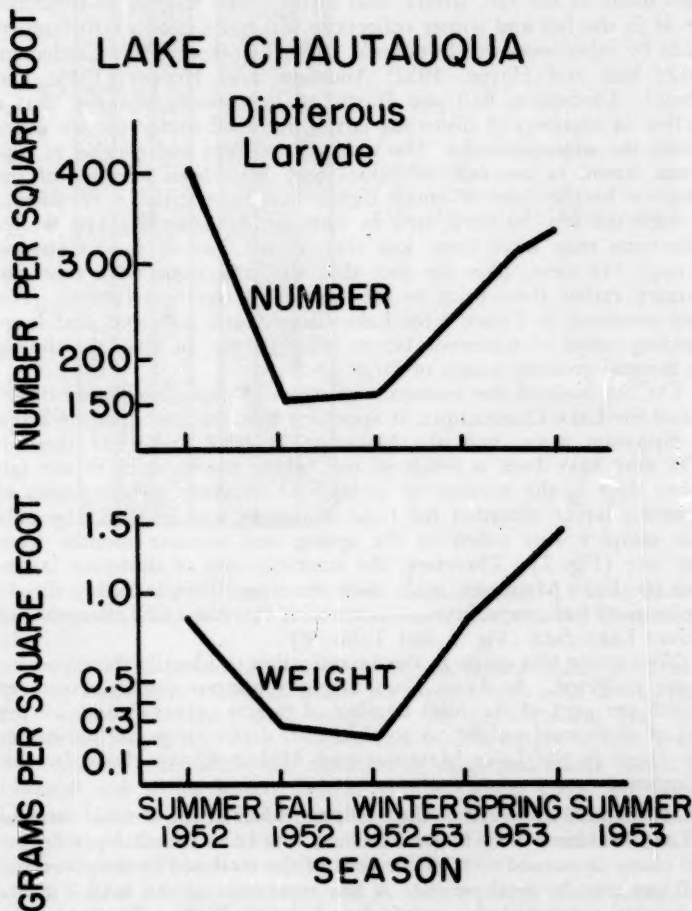


Fig. 8.—Seasonal fluctuations of standing crops of dipterous larvae at Lake Chautauqua, Illinois (1952-53).

son (1928). It will be noted in Figure 7 that some increase occurred in the dipterous larvae population in Quiver Lake following the decline that occurred in the mollusca population after 1952. Dipterous larvae populations in Lake Chautauqua and Lake Matanzas were evidently benefited by the scarcity of snails in those lakes.

Considerable seasonal variation was found to occur in the dipterous larvae population in Lake Chautauqua (Fig. 8), during the 1952-53 period. The summer collections in both 1952 and 1953 contained greater numbers and weights of dipterous larvae than did the collections made in the fall, winter, and spring. The scarcity of dipterous larvae in the fall and winter collections was quite contrary to findings made by other workers (Lundbeck, 1926; Eggleton, 1931; Lindeman, 1942; Ball and Hayne, 1952; Anderson and Hooper, 1956; and others). Lindeman, Ball and Hayne all mentioned, however, that a decline in numbers of dipterous larvae occurred under the ice cover during the winter months. The reduced numbers and weights of dipterous larvae in our fall collections may have been a result of the presence in the lake of small dipterous larvae capable of passing through the No. 30 sieve used in washing the samples. The winter collections may have been low due to the loss of larvae passing through the sieve, plus the fact that the collections were taken in January rather than prior to the time ice cover was formed. The data presented in Figure 8 for Lake Chautauqua indicated that large standing crops of dipterous larvae were present in the lake during the normal growing season of fishes.

On the basis of the seasonal variations of dipterous larvae determined for Lake Chautauqua, it appeared that the low standing crops of dipterous larvae at Lake Matanzas in 1952 and 1954 through 1956 may have been a result of our taking the samples in the fall rather than in the summer or spring. The highest standing crop of dipterous larvae recorded for Lake Matanzas was in 1953, the only year samples were taken in the spring and summer months from that lake (Fig. 7). Therefore, the standing crop of dipterous larvae data for Lake Matanzas, other than the year 1953, probably should not be used for comparative purposes with the Lake Chautauqua and Quiver Lake data (Fig. 7 and Table V).

No attempt was made in this investigation to identify the dipterous pupae collected. At Lake Chautauqua dipterous pupae accounted for 0.6 per cent of the total number of insects collected and 2.0 per cent of their total weight. A total of four dipterous pupae altogether was taken in the Lake Matanzas and Middle Quiver Lake benthic collections.

**MOLLUSCA:** — All of the mollusca taken in the benthic samples at Lake Matanzas were fingernail clams. At Lake Chautauqua fingernail clams amounted to 97.0 per cent of the mollusca by numbers and 99.0 per cent by total weight. A few specimens of the snail *Valvata tricarinata* comprised the remainder of the mollusca collections from Lake Chautauqua.

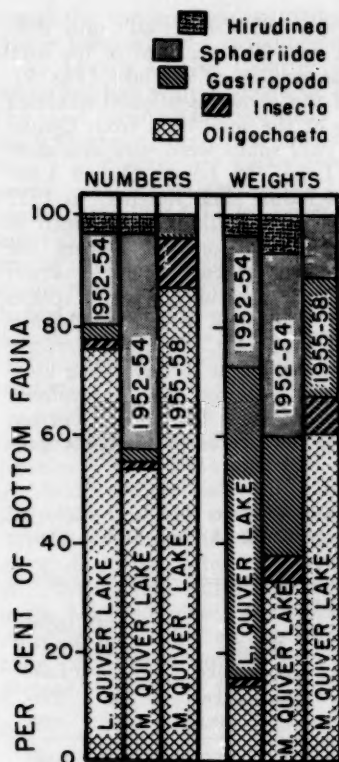


Fig. 9. — Composition of bottom fauna organisms at Lower Quiver Lake (1952-54) and Middle Quiver Lake (1952-54; 1955-58), Illinois.

Fingernail clams disappeared from the collections at Lake Matanzas after 1953, and after 1954 they became scarce at Lake Chautauqua (Fig. 7).

In 1952 fingernail clams were extremely abundant in Middle Quiver Lake, amounting to 2,286 per square foot with a weight of 6.71 grams (excluding shell weights). In the following year their numbers dropped to 103 per square foot with a weight of 0.48 grams. Between 1954 and 1958 the numbers of fingernail clams varied between 0 and 50 per square foot in Middle Quiver Lake. At Middle Quiver Lake in the 1952-54 period fingernail clams comprised 59.4 per cent of the total weight of mollusca (Fig. 9); whereas, in the 1955-58 period they amounted to only 29.5 per cent.

A similar decline also occurred in the fingernail clam population of Lower Quiver Lake. The fingernail clam population at that lake dropped from 1,115 per square foot in 1952 to 54 in 1953 and to 0

in 1954. At Lower Quiver Lake in the 1952-54 period (only data available) fingernail clams comprised only 29.2 per cent of the total weight of mollusca collected from that portion of the lake (Fig. 9).

Snails comprised the remainder of the above mentioned mollusca weights at Quiver Lake. A summary of the snail data from Quiver Lake is presented in Table VII. In 1952 snails were very abundant in both Lower and Middle Quiver Lake. At Lower Quiver Lake snails decreased from 10.76 grams (excluding shell weights) in 1952 to 6.07 grams in 1954. All of the species of snails there declined in abundance with the exception of *Pleurocera acuta*. During the 1952-54 period at Lower Quiver Lake the species *Campeloma decisum* comprised 45.6 per cent of the total snail weight. This species comprised only 11.7 per cent of the total snail weight in Middle Quiver Lake. The difference in abundance of *Campeloma decisum* between the two sections of the lake was thought to have been associated with water current. Baker (1928) reported that *Campeloma decisum* was found in the presence of a current. The lack of current in Middle Quiver Lake at times of low water levels probably pre-

TABLE VII.—Species composition, average numbers and wet weights of snails per square foot at Lower Quiver Lake (1952-54) and Middle Quiver Lake (1952-54 and 1955-58), Illinois

Species	1952-1954				1955-1958	
	Lower Quiver Lake		Middle Quiver Lake		Middle Quiver Lake	
	No.	Per-cent	No.	Per-cent	No.	Per-cent
<i>Valvata tricarinata</i>	*	—	1	1.7	0	—
<i>V. lewisi</i>	*	—	0	—	0	—
<i>Viviparus contectoides</i>	8	9.8	2	3.5	*	—
<i>V. intertextus</i> ill.	4	4.9	1	1.8	0	—
<i>Lioplax subcarinata</i>	*	—	*	—	0	—
<i>Campeloma integrum</i>	1	1.2	0	—	*	—
<i>C. rufum</i>	*	—	0	—	0	—
<i>C. decisum</i>	17	20.7	1	1.8	0	—
<i>Amnicola limosa</i>	2	2.4	1	1.8	0	—
<i>Cincinnatia emarginata</i>	31	37.8	48	84.2	0	—
<i>Pleurocera acuta</i>	19	23.2	3	5.2	1	100.0
Undetermined young	*	—	*	—	0	—
Total	82	100.0	57	100.0	1	100.0
Weight in grams (excluding shells)	11.45		1.68		0.48	

\* Denotes less than 0.5 organisms per square foot.

vented the species from occurring as abundantly as it did in Lower Quiver Lake where a current was always present.

At Middle Quiver Lake in 1952 the snail population was 124 per square foot with a weight of 3.35 grams (excluding shell weight). The snail population dropped in 1953 to 44 per square foot (weight was 0.87 grams) and from 1954 through 1957 the population ranged from 1 to 2 snails per square foot (weight ranged from 0.39 to 1.01 grams). Table VII reveals the changes that occurred in the various species of snails at Middle Quiver Lake between the periods of 1952-54 and 1955-58. After 1952 the small snail *Cincinnatia emarginata* began to decline in numbers, and by 1954 the species was completely absent from the collections (Fig. 10). The species followed a similar decline in the collections from Lower and Upper Quiver Lake. Collections made in the years after 1953 failed to reveal the presence of *Cincinnatia emarginata* in any of the three sections of the lake sampled.

**HIRUDINEA:**—Leeches comprised only a small part of the bottom fauna collections from Lake Chautauqua and Lake Matanzas (Tables V and VIII and Fig. 6). In 1952 leeches were abundant in Middle Quiver Lake where the standing crop was 134 per square foot. Most of the leech population was comprised of *Helobdella stagnalis*. A drastic decline occurred in the leech population in Middle Quiver Lake after 1952 which paralleled the declines of *Cincinnatia emarginata* and fingernail clams (Fig. 10). No leech was taken in the Middle Quiver Lake collections after 1954. Richardson (1928) noted in his studies on the Illinois River that increases in fingernail clam populations possibly were checked by leech predation. In the present study (Fig. 10) it appeared that the decline and final dis-

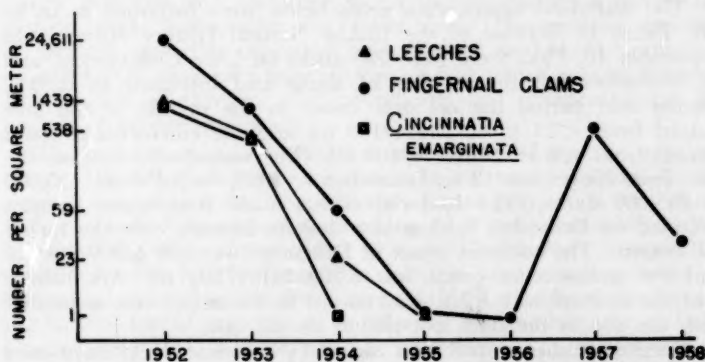


Fig. 10.—Predator-prey relationship is shown between leeches and small mollusca at Middle Quiver Lake, Illinois (1952-58). The number of organisms per square meter is plotted on semi-log paper. (Less than 1 organism per square meter is 0.)

appearance of leeches in Middle Quiver Lake was related to the collapse of the small mollusca populations which had probably served as prey for the leeches.

#### BOTTOM FAUNA IN RELATION TO WATERFOWL

In late winter and early spring of 1953 lesser scaup ducks (*Athya affinis*) occurred abundantly on Quiver Lake. The maximum number of scaup ducks present at one time on the lake that year was about 20,000. Since 1953 very few scaup ducks have used the lake. The maximum number we have seen on the lake since 1953 has been less than 1,000 birds.

The lesser scaup ducks were observed on numerous occasions by us in early 1953 to be diving apparently for small mollusca which were then abundant in the lake. Bent (1951) and Cottam (1939) listed small mollusca as part of the diet of the lesser scaup duck. We believe that the scarcity of scaup ducks on Quiver Lake after early 1953 was associated with the disappearance of small snails and the decline of fingernail clams that occurred at that time (Fig. 10). The temporary slight increase that occurred in the fingernail clam population in 1957 (Fig. 10) did not result in an increased usage of the lake by scaup ducks.

#### POLLUTION CAUSED BY WATERFOWL

Lake Chautauqua is used by large concentrations of migrating waterfowl chiefly during the months of late October, November, and December. Mallards (*Anas platyrhynchos*) comprise the bulk of the waterfowl that use the lake. These migrating birds do most of their feeding in local fields on corn that is knocked to the ground by mechanical corn pickers (Bellrose, 1954).

The waterfowl census data given below were furnished to us by Mr. Frank C. Bellrose of the Illinois Natural History Survey. On September 10, 1953 there were 200 ducks on Lake Chautauqua, and by November 5th the number of ducks had increased to 62,000. During that period the coliform count in the middle of the lake ranged from <23 to 60 MPN/100 ml and the enterococcus count ranged from <6 to 23 MPN/100 ml. The waterfowl count on the lake from November 12 to December 7, 1953, varied from 195,000 to 205,000 ducks. The bacterial counts made from water samples collected on December 8, showed a definite increase over the earlier fall counts. The coliform count in December was 230 MPN/100 ml and the enterococcus count was 6,200 MPN/100 ml. We believe that the increase in the bacterial counts in December was associated with the rise in the duck population on the lake.

Detailed studies of pollution caused by domestic ducks have been reported by various persons working in New York State. Redfield (1952) estimated that 2.7 million pounds of nitrogen and 0.82 million pounds of phosphate are available annually from duck farms on tributaries of Moriches Bay and on the Carmans River, New

York, where 4 million domestic ducks are produced annually. From this same area Ryther (1954:207) found that: "Although the bays were heavily enriched only during the duck growing season, relatively high concentrations of nutrients appear to be present throughout the year, presumably from the decomposition of the rich sediments in the tributaries receiving the duck farm effluents." Stall and Melsted (1951:12) reported concerning the sediment characters of Lake Chautauqua, Illinois, that: "The total carbon and total nitrogen values are extremely high, indicating an accumulation of organic matter in the lake far in excess of any amounts that could be accounted for through soil erosion. These large accumulations of nitrogen and carbon must, therefore, be attributed to wildlife excreta." The water analyses for Lake Chautauqua did not reflect an increase in nutrient materials during the height of duck usage on the lake in the late fall of 1953.

In the fall, winter, and spring of 1954-55, 20,000,000 duck-days were spent on Lake Chautauqua. It was considered that these ducks spent a part of their time on other waters or in cornfields feeding. Mr. Bellrose believed that a conservative estimate of actual use of the lake by the ducks would have been 80 per cent of the total duck-day value or 16,000,000 continuous duck-days on the lake. In the studies made by the New York State Water Pollution Board in Suffolk County (Sanderson, 1953) it was found that the raw wastes produced daily by 1,000 domestic ducks contained an average of 5.7 pounds total nitrogen, 7.6 pounds of total phosphate, and 3.6 pounds of soluble phosphate. Since domestic ducks are fed large quantities of prepared feeds by man their wastes would be expected to be higher in nutrients than those of wild ducks. In order to apply the above domestic duck waste values to wild ducks at Lake Chautauqua we arbitrarily used 0.50 as a correction factor to compensate for differences in food intake and smaller size of the birds. The resulting estimate of fertilizer materials deposited by waterfowl in Lake Chautauqua on a per acre basis each year in the 1954-55 period was as follows: 12.8 pounds of nitrogen, 17.1 pounds of total phosphate, and 8.1 pounds of soluble phosphate.

Ducks were on Lake Matanzas and Quiver Lake for approximately 100,000 duck-days each year. In an earlier section of this paper it was shown that the dipterous larvae population was much higher in Lake Chautauqua than in the other two lakes studied. We believe that the nutrients added to Lake Chautauqua annually by waterfowl were largely responsible for the large standing crops of dipterous larvae. Jackson and Starrett (1959) considered the following factors also of importance in affecting the productivity of Lake Chautauqua: (1) lack of summer stagnation; (2) shallowness of the lake; and (3) addition of nutrients from the river.

#### SILTATION

Siltation that is occurring in the Illinois River flood plain lakes

is drastically reducing their storage capacities. In the three lakes studied silt has been deposited at a high annual rate since the early 1930's (Jackson and Starrett, 1959).

Ellis (1931) discussed the adverse effects of silt upon snails in the Mississippi River. We have theorized that the scarcity of snails in Lake Chautauqua and Lake Matanzas may have been caused by siltation. In those lakes current was seldom perceptible, whereas in Quiver Lake current was present except during low river stages. The absence of current in Lake Chautauqua and Lake Matanzas may permit suspended silt particles to settle over young snails and smother them. In Quiver Lake the current may have prevented the silt from settling at a rate sufficient to suffocate young snails. The results of the present study suggest that the scarcity of snails in Lake Chautauqua and Lake Matanzas may allow dipterous larvae to utilize the increased enrichment of bottom soils caused by human, duck and silt pollution.

In 1952 and 1953, the bottom fauna at Middle Quiver Lake was rich in mollusca and supported only a small dipterous larvae population, a situation similar to that found in the earlier years of "cleaner water" in the Lower Illinois River (Richardson, 1921a). In contrast, large dipterous larvae populations occurred in Lake Chautauqua and Lake Matanzas in 1953.

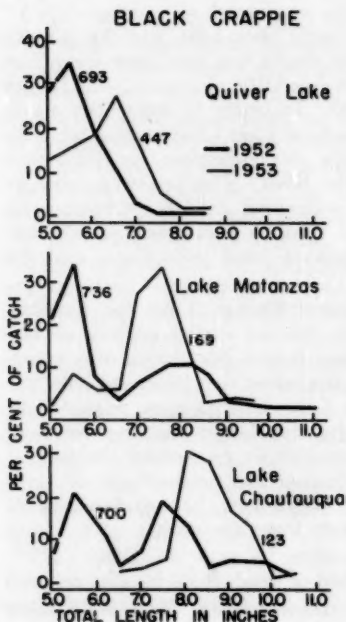


Fig. 11. — Length-frequency distribution of black crappies taken in 1-inch wing net collections during early fall months (1952 and 1953) at Quiver Lake, Lake Matanzas and Lake Chautauqua, Illinois. Number of fish measured accompany each graph.

An attempt was made to correlate growth of the black crappie with the abundance of dipterous larvae. Length-frequency data for black crappies collected in the fall months of 1952 and 1953 from Quiver Lake, Lake Matanzas and Lake Chautauqua are presented graphically in Figure 11. We were not able to age the black crappies from Quiver Lake with any degree of accuracy; however, rate of growth of black crappies collected from Lake Matanzas and Lake Chautauqua was considered good. The length-frequency graphs indicated that Lake Matanzas and Lake Chautauqua contained black crappies of sizes useful to anglers (8 inches), whereas, the black crappies in Quiver Lake were mostly of undesirable sizes. We believe the poor growth of black crappies in Quiver Lake was related, at least in part, to the scarcity of dipterous larvae in that lake. On the other hand, we hypothesize that the abundance of dipterous larvae in Lake Chautauqua and Lake Matanzas may have been an important factor to the rapid growth of black crappies in those lakes.

#### CHANGES IN BOTTOM FAUNA

The benthic studies made in Lower Quiver Lake in the 1952-54 period are of particular interest here since that section of the lake is actually a part of the Illinois River investigated by Richardson (1928) between 1913 and 1925 (Figs. 1 and 3). Richardson found in the cleaner water period of 1913-15 that snails formed an impor-

TABLE VIII.—Species composition and average numbers of leeches per square foot at Lake Matanzas, Middle Quiver Lake and Lake Chautauqua, Illinois

Species	Lake Matanzas <sup>1</sup>		Quiver Lake <sup>2</sup>		Lake Chautauqua <sup>1</sup>	
	No.	Per-cent	No.	Per-cent	No.	Per-cent
<i>Helobdella stagnalis</i>	*	—	21	84.0	1	33.3
<i>H. elongata</i>	1	100.0	3	12.0	2	66.7
<i>H. lineata</i>	0	—	*	—	0	—
<i>Erpobdella punctata</i>	*	—	1	4.0	0	—
<i>Glossiphonia complanata</i>	0	—	*	—	0	—
<i>Placobdella montifera</i>	*	—	*	—	0	—
<i>Myzobdella moorei</i>	0	—	*	—	*	—
<i>Actinobdella</i>						
<i>inequiannulata</i>	0	—	0	—	*	—
<i>Dina</i> sp.	0	—	*	—	0	—
Undetermined	0	—	*	—	0	—
Total	1	100.0	25	100.0	3	100.0

<sup>1</sup> 1952-56.

<sup>2</sup> 1952-58.

\* Denotes less than 0.5 organism per square foot.

tant part of the bottom fauna in all reaches of the river between Chillicothe and Beardstown. The snails collected in the 1913-15 period included at least one-half dozen species sensitive to pollution. Some of those species were: *Viviparus contectoides*, *Lioplax subcarinata*, *Amnicola emarginata* (probably *Cincinnati emarginata*) and *Amnicola limosa*. By 1920 these more sensitive species were practically wiped out by pollution from the deeper open water of the river between Chillicothe and Beardstown. Richardson (1928:430) stated that: "Below Peoria, in the 10 miles between Havana and Liverpool, where the combined *Gastropoda* had averaged 496 per square yard in 1915, they rose in 1925 to a bit less than 40, from just half that number at the recorded low point five years before. The fact that more than half of the specimens taken in this section in 1925 were *Vivipara contectoides*, however, (the rest being *Campe-loma subsolidum*) seems to reflect to some extent the results of the previously mentioned improvement in the bottom dissolved oxygen supply below Copperas Creek Dam since 1923." Further improvement in the condition of the river has occurred since 1925 as was shown by our collections from Lower Quiver Lake in the 1952-54 period (Table VII) where water-breathing snails averaged 738 per square yard.

Richardson (1921a) took bottom samples at Lake Matanzas in the summer of 1915 and at Quiver Lake in 1914, 1915 and 1920. A comparison is made in Table IX of Richardson's bottom samples

TABLE IX.—Numbers of bottom fauna organisms per square yard at Lake Matanzas, Illinois, 1915 and 1953 (Summer)<sup>1</sup>

Organisms	Year		
	1915 <sup>2</sup> Number	1915 <sup>3</sup> Number	1953 Number
<i>Campeloma subsolidum</i>	0.0	5.0	0
<i>Pleurocera</i> sp.	0.0	1.6	0
<i>Viviparus contectoides</i>	0.0	8.3	0
<i>Valvata</i> spp.	14.4	3.3	0
<i>Sphaeriidae</i>	269.9	63.3	180
Sub-total	284.3	81.5	180
Dipterous larvae and pupae	23.3	2.3	2,790
<i>Hexagenia</i> , etc., nymphs	0.0	6.6	0
<i>Caenis</i> nymph	0.0	3.3	0
Leeches	30.7	13.8	63
Oligochaeta	4.4	0.0	11,007
Total	342.7	107.5	14,040

<sup>1</sup> 1915 data after Richardson (1921a:506-507).

<sup>2</sup> Depth, 6.5 to 8.5 feet, no vegetation.

<sup>3</sup> Depth, 2 to 6 feet, some vegetation at all stations.

from Lake Matanzas with our collections taken there in 1953. It is apparent from Table IX that some major changes have occurred in the bottom fauna at Lake Matanzas since 1915. In that year snails were common in the lake, whereas, in 1953 none were taken in our samples. Numbers of *Oligochaeta* and dipterous larvae have greatly increased in the lake since 1915. Richardson collected 6.6 *Hexagenia* sp. nymphs per square yard in one series of collections from Lake Matanzas in 1915, while through the entire 1952-56 period only 1 specimen of *Hexagenia* was taken from that lake. Possibly the reduction that occurred in mayfly nymphs in the lake was caused by competition with dipterous larvae, as the latter greatly increased in the lake sometime after 1915.

In Table X a comparison is made between Richardson's (1921a) 1914 and 1915 bottom samples from Quiver Lake and our 1952 and 1954 samples from Middle Quiver Lake. In 1914 and 1952 mollusca were abundant in Quiver Lake; however, species of small snails and

TABLE X.—Numbers of bottom fauna organisms per square yard at Middle Quiver Lake, Illinois, 1914-15 and 1952 and 1954<sup>1</sup>

Organisms	Year			
	1914 No.	1915 No.	1952 No.	1954 No.
<i>Campeloma subsolidum</i>	24.7	0.0	0	0
<i>Lioplax subcarinata</i>	11.1	0.0	3	0
<i>Viviparus contectoides</i>	48.2	7.1	45	9
<i>Pleurocera</i> sp.	1.1	0.0	45	9
Other species of large snails	0.0	0.0	63	3
<i>Amnicola emarginata</i>	42.3	0.0	0	0
<i>Amnicola limosa</i>	8.2	16.0	3	0
<i>Valvata</i> spp.	9.4	0.0	3	0
<i>Physa</i> , small	7.6	0.0	0	0
Other species of small snails <sup>2</sup>	0.0	0.0	963	0
Sphaeriidae	50.2	1.0	20,574	54
Sub-total	202.8	24.1	21,699	75
Dipterous larvae and pupae	38.9	176.3	135	411
Trichoptera larvae	0.5	0.0	9	0
<i>Hexagenia</i> nymph	0.5	0.0	27	72
Agrionid nymph	1.1	2.1	0	0
Libelluid nymph	1.6	0.0	0	0
Leeches	37.6	11.9	1,215	24
Oligochaeta	11.7	0.0	13,716	4,347
Coleoptera larvae	0.0	0.0	0	3
Total	294.7	214.4	36,801	4,932

<sup>1</sup> 1914-15 data after Richardson (1921:505-506).

<sup>2</sup> Refers to *Cincinnatia emarginata* which is probably the same species Richardson identified as *Amnicola emarginata*.

finger nail clams (chiefly young) were more abundant in the lake in 1952 than in 1914. The species *Cincinnatia emarginata* which occurred so abundantly in the 1952 collections (Fig. 10) was probably the same species that Richardson identified in his 1914 collections as *Amnicola emarginata*. *Campeloma subsolidum*, later referred to as *Campeloma crassulum* (Baker, 1928), occurred abundantly in Richardson's 1914 collections but was not taken in the present study. The large snail *Viviparus contectoides* was common in collections from Quiver Lake in 1914 and 1952. Dipterous larvae were not abundant in the lake either in 1914 or 1952. The striking difference in the bottom fauna at Quiver Lake between the years 1914 and 1952 was the abundance of worms in the 1952 collections (Table X). In 1920 Richardson (1921b) found that Quiver Lake had only 48 worms per square yard on mud bottom and that the lake did not show the great increase in worms he found elsewhere along the river, following the severe pollution conditions that existed there during World War I.

Richardson's 1915 samples at Quiver Lake showed a sharp decline in the small mollusca population from the previous year (Table X). Similarly the mollusca population was greatly reduced at Quiver Lake in the 1952-58 period (Fig. 7 and Table X). Richardson (1921a) concluded that the severe decline in small mollusca in the 1914-15 period was due to some unexplained mortality. It is doubtful if the decline of mollusca in the 1952-58 period in Quiver Lake was related to an increase in pollution accompanied by a reduction in dissolved oxygen, since the mayfly nymph *Hexagenia limbata* remained abundant in the lake (Table X). Richardson (1928) considered *Hexagenia bilineata* an important clean water species and found it to be common in the river near Havana in the 1913-15 period and earlier. In 1920 Richardson failed to take that species of mayfly from the river 4 miles below Havana. Hunt (1953) stated that nymphs of *Hexagenia limbata* were unable to withstand stagnation conditions where the dissolved oxygen content of the water dropped below 1 ppm. We are, therefore, of the opinion that possibly the declines in mollusca populations at Quiver Lake noted by Richardson in 1915 and presently by ourselves were natural declines following periods of overpopulation of mollusca rather than a result of an oxygen deficiency caused by some form of pollution. However, there is also the possibility that one or more of the new organic chemical exotics in the river, such as detergents, could have adversely affected the molluscan population in Quiver Lake in 1953.

The great increases in worms that have occurred at Lake Matanzas and Quiver Lake since 1915 evidently resulted from pollution and siltation.

#### SUMMARY

This investigation was conducted to show the effects that various types of pollutants have had upon the bottom fauna organisms in

three Illinois River flood plain lakes. The lakes studied were in the vicinity of Havana, Illinois. Between 1952 and 1958, 363 bottom samples were taken with a 6 x 6-inch Ekman dredge. Results of chemical analyses indicated that all three lakes were rich in nutrients.

The annual standing crop of benthic organisms varied considerably in the three lakes. The average standing crop per square foot was: 495 organisms and 0.90 grams in Lake Matanzas; 1,108 organisms and 4.44 grams in Middle Quiver Lake; and, 886 organisms and 1.50 grams in Lake Chautauqua.

Dipterous larvae were never abundant in the collections from Quiver Lake; however, they formed an important part of the benthic collections from Lake Chautauqua and Lake Matanzas. Fertilizing materials deposited by migratory waterfowl together with the scarcity of snails were considered as factors contributing to the development of large standing crops of dipterous larvae in Lake Chautauqua. Species of the genera *Pelopia*, *Procladius* and *Coelotanytus*, were common dipterous larvae in the collections from all three lakes. *Chaoborus* sp. was the most common dipterous larva taken at Lake Matanzas, whereas, this form was scarce in the collections from the other two lakes studied.

On the basis of numbers, Oligochaeta comprised over 60 per cent of the bottom fauna from all three lakes.

*Hexagenia limbata* nymphs represented 75.4 per cent of the weight of the immature insects taken in the collections from Middle Quiver Lake. This species did not occur in the collections from Lake Chautauqua, and only one specimen of *Hexagenia* sp. was collected at Lake Matanzas.

Fingernail clams and water-breathing snails flourished in Quiver Lake in 1952. After 1952 the molluscan population of that lake declined sharply. Mollusca formed only a minor part of the bottom fauna of Lake Chautauqua and Lake Matanzas.

Leeches were abundant in Quiver Lake in 1952; however, a drastic decline occurred after 1952 which tended to parallel the decline of the small mollusca population. No leech was taken from Middle Quiver Lake after 1954.

A reduction in numbers of lesser scaup ducks using Quiver Lake occurred following a decline in the population of small mollusca of that lake.

Findings in the present study reveal some drastic changes in the bottom fauna of Quiver Lake and Lake Matanzas since 1914 and 1915. The most drastic change since that time has been the great increase in Oligochaeta. At Lake Matanzas the Oligochaeta population jumped from 4.4 per square yard in 1915 to 11,007 in 1953. A similar change has occurred in Quiver Lake. At Lake Matanzas the mollusca population has become greatly reduced since 1915 and the dipterous larvae population has increased. Siltation and other forms of pollution were considered important factors in the drastic changes that have occurred in the bottom fauna of the lakes studied.

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## Mammals of the Santa Catalina Mountains, Arizona

KENNETH I. LANGE\*

This paper is a compilation of mammal records from the Santa Catalina Mountains, Pima and Pinal counties, Arizona, based on the author's field work in the area and that of earlier investigators. The Santa Catalina Mountains are about ten miles north of Tucson and are between  $32^{\circ} 15'$  and  $32^{\circ} 35'$  north latitude and  $110^{\circ} 30'$  and  $111^{\circ}$  west longitude. The boundaries, as herein defined in reference to landmarks, are as follows: Reddington Pass in the southeast; Tanque Verde and Rillito creeks, including Fort Lowell, in the south; the Oracle and Florence highway in the west; and east along State Highway 77 to Oracle in the north.

Among mammal collections from this area, those by the following individuals and institutions may be mentioned: (1) E. W. Nelson and other Biological Survey personnel (specimens reported in various issues of the *North American Fauna*), (2) W. W. Price (in Allen, 1895), (3) Edgar A. Mearns and Frank X. Holzner on the Mexican Boundary Survey (in Mearns, 1907), (4) J. Kenneth Doult for Carnegie Museum (Doult, 1934), (5) Lee R. Dice and Philip M. Blossom for the University of Michigan (in Dice and Blossom, 1937), (6) Kansas University in 1952, and (7) the University of Arizona.

Collecting and field work has been concentrated in the following localities: (1) Camp or Fort Lowell, about 2000 feet, an abandoned military post on the south bank of Rillito Creek, about six miles from the base of the mountains; cottonwoods and willows along the creek, desert shrubs on the adjoining outwash plain (bahada); (2) Molino Basin, 4000 to 4200 feet, south face; desert grassland; (3) Oracle, 4500 feet, a town in Pinal County; desert bahadas and slopes, desert grassland; (4) Peppersauce Canyon, about 4600 feet, north face, some eight miles southeast of Oracle; riparian vegetation, mainly sycamores, along Peppersauce Creek, evergreen woodland (encinal) on the hill-sides; (5) mouth of Pima Canyon, about 3200 feet, south face; desert bahadas and rocky slopes; (6) Reddington Pass, 4000 to 4300 feet, the pass between the Santa Catalina Mountains and the Rincon Mountains in the southeast; rocky slopes; (7) Lower and Upper Sabino Canyons, 3000 to 3400 feet, south face; bahadas and rocky slopes; (8) Soldier Camp area, 7700 to 8000 feet, south face; pines and firs; (9) mouth of Soldier Canyon, 3000 feet, south face; bahadas and slopes; (10) near Stratton Mine, 4600 feet, north face; encinal; (11) Summerhaven area, 7600 to 8000 feet, south face; pines and firs.

The following abbreviations are used with the records of occurrence for each species (the number with each abbreviation in the following list refers to the number of specimens from the Santa Catalina Mountains herein reported from

\* Present address: 3168 18th St., N.W., Washington 10, D.C.

that collection): AMNH—American Museum of Natural History, New York (14); BS—United States Fish and Wildlife Service, Biological Survey Collections, Washington, D. C. (212); Carnegie—Carnegie Museum, Pittsburgh, Pennsylvania (61); CNHM—Chicago Natural History Museum (2); DRD—Donald R. Dickey private collection (4); KU—Museum of Natural History, University of Kansas, Lawrence (41); LACM—Los Angeles County Museum (3); MVZ—Museum of Vertebrate Zoology, University of California (36); SDSNH—San Diego Society of Natural History (7); Stanford—Department of Biology, Stanford University, Palo Alto, California (1); UA—Department of Zoology, University of Arizona, Tucson (330); UM—Department of Zoology, University of Michigan, Ann Arbor (probably around 250); and USNM—United States National Museum, Washington, D. C. (140).

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#### PHYSIOGRAPHY AND VEGETATION

Tucson is situated at an elevation of about 2400 feet, whereas the basal elevation of the Santa Catalina Mountains is 3000 to 3500 feet. This rise is caused by the ascent in the bahadas, or outwash plains, which form the floor of the Santa Cruz Valley. Mt. Lemmon, 9163 feet, is the highest point of the Santa Catalinas and is located near the west end of the main ridge. Reddington Pass, at 4300 feet, connects the Catalinas in the southeast with the Rincon Mountains. The Canada Del Oro and the San Pedro River receive the north face drainage, and Rillito Creek receives the south face drainage. The Rillito drains into the Santa Cruz River; both the Santa Cruz and San Pedro are tributaries of the Gila River, but seldom have sufficient flow to reach it. Topography is steep and rugged; the major streams possess steep gradients. There are no mountain meadows or parks in the Catalinas.

Doutt (1934:243-44) pointed out that the Catalinas belong physiographically to the Mexican Highland Section, but, since they are separated from the other local ranges by the San Pedro and Gila

Rivers, they are more closely related to the Mexican Cordillera than to the Rocky Mountains. This land relationship extends also to the flora and fauna.

The vegetation of the Catalinas consists of (1) desert, (2) encinal, and (3) forest (after Shreve, 1915). Characteristic plants of the desert bahadas are creosote-bush (*Larrea tridentata*), various prickly pears (*Opuntia*), paloverdes (*Cercidium*), mesquites (*Prosopis*), and species of *Acacia*. On the desert slopes above the bahadas the following plants become abundant: ocotillo (*Fouquiera splendens*), *Agave palmeri*, *Agave schottii*, *Yucca macracarpa*, desert-spoon (*Dasyliiron wheeleri*), bear-grass (*Nolina*), manzanita (*Arctostaphylos*), and California rosewood (*Vanquelinia californica*). Saguaros are generally distributed on the bahadas and slopes. The ground cover of the desert slopes is more extensive than in the bahadas due to the replacement of many desert species by grasses and shrubs.

On the south face of the mountains, at about 4000 feet, desert begins to merge into encinal (evergreen woodland). This transition requires only a few hundred feet of elevation, and is in reality a compressed desert grassland (C. H. Lowe, Jr., personal communication). It can be observed at such areas as Molino Basin. Mesquite or desert grassland is well developed on the north and east faces of the mountains at about the same elevation, mainly because of more gentle slope. Encinal in the Catalinas is an admixture of evergreen oaks (*Quercus oblongifolia*, *Q. arizonica*, *Q. emoryi*), junipers, and pinyon pines. It begins at about 4500 feet and grades into ponderosa pine (*Pinus ponderosa*) forest at about 6500 feet. The elevational limits of encinal depend on such factors as slope exposure and topographical irregularities (Shreve, 1922). A pine-oak woodland between oaks and ponderosa pine may be recognized.

Ponderosa pine is the dominant tree on south slopes from some 6000 feet to the summit of Mt. Lemmon. The subdominants of the ponderosa pine forest are ceanothus (*Ceanothus fendleri*), chokecherry (*Prunus virens*), silver-leaved oak (*Q. hypoleucoides*), and a deciduous species of oak (*Q. gambeli*) (Lowe, personal communication). Clumps of muhly (*Muhlenbergia longiligula*, *M. montana*) also are characteristic.

Firs (*Pseudotsuga taxifolia*, *Abies concolor*, *A. lasiocarpa arizonica*) occur in mixed stands with southwestern white pine (*P. strobiformis*) and ponderosa pine on north slopes up to about 7500 feet, at which elevation ponderosa pine begins to drop out. Quaking aspen (*Populus tremuloides*) is associated with the fir forest. Coniferous forest in the Catalinas thus consists of two segments, ponderosa pine forest and fir forest. There is no timberline.

Riparian habitats are also present. They may be recognized at the lower elevations by such deciduous trees as cottonwood (*Populus fremonti*), willows (*Salix*), sycamore (*Platanus wrightii*), walnut (*Juglans major*), and ashes (*Fraxinus*). In the oak and coniferous growth at the higher elevations, these are replaced by maples (*Acer*

*glabrum*, *A. grandidentatum*, *A. negundo*) and alders (*Alnus*).

See Lange (1959) for photographs of the study area. Figure 5 in that paper is a view in the northern foothills of the Catalinas, Figure 6 is a view of creosote-bush flats, and Figure 7 shows the vegetation at 6000 feet elevation in the Bear Canyon area, south face.

#### ACCOUNTS OF SPECIES AND RECORDS OF OCCURRENCE

The records for each species and subspecies are arranged by elevation, insofar as possible. The following is a list of specimens and records known to the author.

1. *Didelphis marsupialis virginiana* Kerr.—The opossum was apparently introduced into the study area in the late 1940's (Hock, 1952).

2. *Sorex vagrans monticola* Merriam.—Total, 6: Summerhaven, 7500 ft., 4 (3, BS; 1, SDSNH); Soldier Camp, 1 (Carnegie); Carter Canyon, 1 (UA).

3. *Notiosorex crawfordi crawfordi* (Coues).—The first specimen of the gray shrew from the Santa Catalina Mountains was collected by J. A. Munro among boulders in ponderosa pine and oak growth on February 10, 1951. Measurements, in millimeters, are: testes, 0; total length, 80; tail, 27; and hind foot, 10. One skull and a left mandible were recovered by the author from some 50 barn owl pellets collected on June 6, 1957, about five miles southwest of Oracle. The collecting locality was a 35 foot shaft along the Burney Mines road, with grasses, jumping cholla, prickly pear, paloverde, mesquites, acacias, and an occasional juniper constituting the major vegetation.

Total, 2: Burney Mines Rd., ca. 5 m. SW Oracle, Pinal Co., 4200 ft., 1 (UA); Bear Canyon, 6000 ft., 1 (J. A. Munro).

4. *Macrotus californicus* Baird.—Total, 4: 9 m. N Tucson [ca. 3000 ft.], 1 (UM); Burney Mines Rd., ca. 5 m. SW Oracle, Pinal Co., 4200 ft., 2 (UA); Virginia Mine, 5000 ft., 1 (UA).

5. *Choeronycteris mexicana* Tschudi.—Total, 5: Tunnels at narrows of Sabino Canyon, 1 (UA); Sabino Canyon, 1 (UA); Alamo Canyon tunnel, 10 mi. N Tucson, 3 (UA).

6. *Myotis yumanensis yumanensis* (H. Allen).—Total, 3: 2 m. N, 7 m. E Tucson, 1 (UA); Castle Rock Ranch, 3 m. N, 16 m. E Tucson, 1 (UA); Lower Sabino Canyon, 3000 ft., 1 (UA).

7. *Myotis velifer* ssp.—The first specimen of the cave myotis from the Catalinas was shot on June 12, 1957, as it was flying along a dry wash on the north face of the mountains.

Total, 1: Burney Mines Rd., ca. 5 m. SW Oracle, Pinal Co., 4200 ft. (UA).

8. *Myotis thysanodes thysanodes* Miller.—The fringed myotis is herein reported for the first time. A female was collected on June 12,

1957, in a south-facing tunnel about one-hundred yards east of the *M. velifer* locality listed above.

Total, 1: Burney Mines Rd., ca. 5 m. SW Oracle, Pinal Co., 4200 ft. (UA).

9. *Myotis volans interior* Miller.—Total, 5: Summerhaven (UM).

10. *Myotis californicus* ssp.—Total, 8: Santa Catalina Mts., 1 (BS); Lower Sabino Canyon, 3000 ft., 1 (UA); Oracle, Pinal Co., 5 (USNM); Summerhaven, 1 (UM).

11. *Myotis subulatus melanorhinus* (Merriam).—Total, 3: Santa Catalina Mts., 1 (AMNH); 2 m. N, 7 m. E Tucson, 1 (UA); Castle Rock Ranch, 3 m. N, 16 m. E Tucson, 1 (UA).

12. *Pipistrellus hesperus* ssp.—The pipistrel is an early-flying, common bat in the study area. Nine were seen in Upper Sabino Canyon between 6:15 and 6:27 PM on September 29, 1956 (sun set at 6:16). About 90 were seen on October 12, 1956, flying down the canyon. This flight lasted from 5:40 to 6:10 PM. Pipistrels were first seen on October 19 and 26, 1956, at 5:45 PM, five minutes before sunset. The Molino Basin specimen was shot in daytime flight in December, 1952.

Total, 6: 2 m. N, 7 m. E Tucson, 1 (UA); Sabino Canyon, 7 m. N, 2 m. E Tucson, 2 (UA); Lower Sabino Canyon, 3000 ft., 1 (UA); Molino Basin, 4300 ft., 1 (KU); 8 m. SE Oracle, 1 (UM).

13. *Eptesicus fuscus pallidus* Young.—W. W. Price, in J. A. Allen (1895: 247), stated that the brown bat was, "Abundant everywhere, from the desert region about Fort Lowell, to the summit of the Chiricahua Mountains [Cochise County], 10,000 feet above sea level."

Total, 15: Ft. Lowell [ca. 2000 ft.], 3 (LACM); 2 m. N, 7 m. E Tucson, 3 (UA); Sabino Canyon, 7 m. N, 13 m. E Tucson, 1 (UA); Burney Mines Rd., ca. 5 m. SW Oracle, Pinal Co., 4200 ft., 1 (UA); 8 m. SE Oracle, 2 (UM); Summerhaven, 1 (UM); Camp Lawton, Mt. Lemmon, 8000 ft., 1 (UA); Santa Catalina Mts., 3 (BS).

14. *Lasiurus borealis teliotus* (H. Allen).—Total, 2: Peppersauce Canyon, 8 m. SE Oracle (UM).

15. *Lasiurus cinereus cinereus* (Palisot de Beauvois).—Total, 2: Binghampton ponds, ca. 5 m. NE Tucson, 1 (UA); Tanque Verde Creek, E Tucson, 1 (BS).

16. *Corynorhinus townsendii pallescens* (Miller).—Total, 10: Burney Mines Rd., ca. 5 m. SW Oracle, Pinal Co., 4200 ft., 6 (UA); tunnel at 4500 ft., 1 (UA); 5-½ m. S, 3 m. W Oracle, 4800 ft., 1 (UA); summit, Mt. Lemmon, 2 (KU).

17. *Antrozous pallidus pallidus* (Le Conte).—Total, 7: 2 m. N, 7 m. E Tucson, 4 (UA); Oracle, 3 (BS).

18. *Tadarida brasiliensis mexicana* (Saussure).—W. W. Price, in Allen (1895:246), remarked that this species was, “. . . exceedingly abundant at Fort Lowell through the month of May. Many specimens were taken in the cornice of the deserted hospital building.”

Total, 3; 2 m. N, 7 m. E Tucson, 1 (UA); Lower Sabino Canyon, 1 (UA); Virginia Mine, 5000 ft., 1 (UA).

19. *Tadarida femorosacca* (Merriam).—Total, 6: 2 m. N, 7 m. E Tucson (UA).

20. *Eumops perotis californicus* (Merriam).—Total, 2: 2 m. N, 7 m. E Tucson (UA).

Of the 17 species of bats recorded above, *Myotis velifer* and *Myotis thysanodes* are listed for the first time. Reference to Table I will show that no bats have been collected in the area during January and February, and only six in the last two months of the year. This reflects on several factors: (1) concentration of collecting in the spring, summer, and fall months; (2) migration of some species; and (3) the apparent absence of hibernacula in the Santa Catalina Mountains.

TABLE I.—The 17 species of bats reported from the Santa Catalina Mountains, showing the sex, month of collection, and approximate elevation in hundreds of feet

Species	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Total
				♂	♀					♂			
				50	30					♀			
<i>Macrotus</i>										42			4
						2♂							
						2♀							
<i>Choeronycteris</i>						35		♀					5
				♀		♀		♀					
<i>Myotis yumanensis</i>				25		25		30					3
<i>M. velifer</i>													
						♀							
<i>M. thysanodes</i>						42							1
						♂							
						4♀							
<i>M. volans</i>						75							5
						♂					♂		
<i>M. californicus</i>						75					30		2
				♀		♀							

TABLE I.—(continued)

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Total
<i>M. subulatus</i>				25		25							2
						♂							
				♀		♀	♂			♂		♂	
<i>Pipistrellus</i>				25		30	45			30		43	6
				♂		6♂							
				3♀		2♀							
				25-	♂	20-	2♀						
<i>Eptesicus</i>				30	42	80	45						15
								♂					
								♀					
<i>Lasiurus borealis</i>							45						2
				♂	♀								
<i>L. cinereus</i>				25	25								2
				♂						2♂			
				2♀		♂	♂	♂		80-		2♂	
<i>Corynorhinus</i>				42		42	48	45		90		42	10
						2♂							
				♂	♀			3♀					
<i>Antrozous</i>				25	25			45					7
				♂ 50						♀			
<i>Tadarida brasiliensis</i>				♀ 25						30			3
						4♂							
						2♀							
<i>T. femorosacca</i>						25							6
						2♂							
<i>Eumops</i>						25							2
Total ♂	-	-	4	10	1	12	3	1	-	4	2	3	40
Total ♀	-	-	3	10	1	12	3	3	1	1	1	-	35

21. *Lepus alleni alleni* Mearns.—W. W. Price found the Allen jackrabbit "... abundant about Tucson and in lower portions of the desert belt." He found it "... on the gravelly hills bordering the Rillito at Fort Lowell, and on the immense mesquite and *Larrea* plains of Tucson." (in Allen, 1895: 201-202). Doult (1934: 267) found *L. alleni* and *Lepus californicus eremicus* equally abundant in the desert regions. Vorhies and Taylor (1933: 480) state that *L. alleni* seems "... to prefer grassy slopes at moderate elevations. The animals seem to like the bahadas or mesas above the giant cactus belt [saguaro cactus], where grasses, mesquites, and catclaws abound. They occur

also, somewhat scattered, on the creosote desert, and even, at times, in the heavy mesquite growth along the valley bottoms. . . . *Lepus alleni* is rarely observed in broken or hilly country." Dice saw three in mesquite grassland six miles southeast of Oracle (Dice and Blossom, 1937: 40). The author has seen Allen jackrabbits at an elevation of 4000 feet in Reddington Pass. The vegetation in this locality consists of scattered oaks and junipers, a few mesquites, clumps of manzanita and bear-grass (*Nolina*), small cacti, and sparse grass. Two *alleni* have been seen in this hilly, rocky country. A critical density of encinal may determine the upper elevational limit of *L. alleni alleni*.

Total, 28: Ft. Lowell, 19 (13, AMNH; 6, BS); Tanque Verde, 1 (KU); Rillito Creek, 5 m. N Tucson, 3 (BS); mouth Bear Canyon, 1 (UM); mouth Soldier Canyon, 1 (Carnegie); Oracle, 3 (2, Carnegie; 1, BS).

22. *Lepus californicus eremicus* J. A. Allen.—W. W. Price (in Allen, 1895: 202) thought that this species was, "The common Jack Rabbit over the entire region to about 7000 feet elevation. In the desert region about Tucson, this species is somewhat supplanted by *Lepus alleni*." Vorhies and Taylor (1933: 480) regarded the distributional relationships of these two species to be as follows: "On the grassy bahadas at altitudes of perhaps 3,500 feet, the antelope jack rabbits [*Lepus alleni*] are usually several times as numerous as the *Lepus californicus* type; but in the mesquites along the valley bottoms, and on the barren creosote bush desert, the *L. californicus* type is usually more numerous." *L. c. eremicus* was reported by Dice and Blossom (1937: 40) to range from the desert to the lower oaks. Doult (1934: 268) found *L. c. eremicus* common in the Catalinas to elevations of 4500 feet. He noted it as less common above 4500 feet and did not find any in the pines and firs.

The race, *eremicus*, seems to be unable to tolerate higher elevations, whereas *L. c. deserticola* and *L. c. texianus* in northern Arizona range to 7500 feet. The upper elevational limits for *L. c. eremicus* and *L. alleni alleni* appear to be about the same in the Catalinas, that is 4,500 to 4,700 feet.

Total, 22: Ft. Lowell, 8 (5, USNM; 3, BS); Tanque Verde, 1 (KU); Rillito Creek, 1 (BS); near Walnut, NW base Catalina Mts., 1 (Carnegie); Soldier Canyon, 5 (Carnegie); Oracle, 4 (2, BS; 2, Carnegie); 2 m. S, 2 m. E Oracle, 4500 ft., 1 (UA).

23. *Sylvilagus audubonii arizonae* (J. A. Allen).—The desert cottontail is an abundant animal in the desert regions, apparently reaching its upper elevational limit in the oaks. Sows (1957: 234-35) discusses the distribution of the desert cottontail and reports that it is found in oak woodland in certain parts of southeastern Arizona. The two University of Arizona specimens come from the lower oaks.

Total, 23: Ft. Lowell, 13 (10, USNM; 3, BS); Tanque Verde, 1 (KU); Oracle, 7 (6, BS; 1, Carnegie); 1½ mi. S Oracle, 4500 ft., 1 (UA); 1½ m. S, 1½ m. W Oracle, 1 (UA).

24. *Citellus spilosoma canescens* (Merriam).—Merriam (1890:

38) designated Oracle in Pinal County as the type locality of *Spermophilus spilosoma macrospilatus*, now regarded as a junior synonym of *C. s. canescens*. The series at his disposal consisted of five topotypes and the holotype. These were again reported in *North American Fauna* number 56, page 126. These are the only spotted ground squirrels known from the study area.

Total, 6: Oracle, Pinal Co., (BS).

25. *Citellus variegatus grammurus* (Say).—Price (in Allen, 1895: 237-38) reported the rock squirrel to be common along brush fences at Fort Lowell in the summer of 1892, but found none in January 1894. Mearns (1907) found it from the low desert to the high mountains and thought it hibernated in winter at the high elevations. Doult (1934: 254) recorded it in rocky situations from 2400 to 9400 feet. Dice and Blossom (1937: 21) found them in rocky areas in the Catalinas. They are common in rocky areas at the lower elevations of Sabino Canyon. The author has seen rock squirrels eating mesquite buds and climbing cottonwoods in desert shrub habitat on the San Xavier Mission, Pima County. There are no rock outcrops in this area.

Total, 31: Santa Catalina Mts., 3 (2, BS; 1, MVZ); Ft. Lowell, 2 (1, BS; 1, USNM); mouth of Soldier Canyon, 1 (Carnegie); Upper Sabino Canyon, 3100 ft., 1 (UA); Pima Canyon, 3500 ft., 1 (BS); Linda Vista Ranch, 2½ m. S Oracle, 1 (UA); 2 m. W Oracle, 1 (UA); Oracle, 5000 ft., 15 (BS); near Soldier Camp, 2 (Carnegie); Summerhaven, 4 (3, UM; 1, SDSNH).

26. *Citellus tereticaudus neglectus* (Merriam).—Price (*op. cit.*) and Mearns (1907) remarked on the abundance of the round-tailed ground squirrel. Dice and Blossom (1937: 21) noted their wide distribution on the sandy desert soils. None have been taken on the north face. *C. variegatus*, *A. harrisi*, and *C. tereticaudus* are conspicuous diurnal mammals in the lower elevations.

Total, 51: Ft. Lowell, 29 (16, BS; 13, USNM); Santa Catalina Mts., 2 (CNHM); Rillito Creek, near Ft. Lowell, 5 m. N Tucson, 2 (1 BS; 1, UM); 5 m. N Tucson, 1 (UM); Tanque Verde, 3 (KU); mouth of Sabino Canyon, 3 (KU); mouth of Soldier Canyon, 7 (Carnegie); Soldier Canyon, 4 (UM).

27. *Ammospermophilus harrisi harrisi* (Audubon and Bachman).—Price (in Allen, 1895: 241) and Mearns (1907) found the Harris ground squirrel a common inhabitant of the lower deserts. Mearns (1907) regarded it as abundant in the valleys, canyons, and river bottoms, and did not find it above 5200 feet elevation in the Santa Cruz Valley. Dice and Blossom (1937: 22) found them in many habitats, but with a spotty distribution.

Total, 68: Ft. Lowell, 5 (USNM); Catalina Mt. foothills, S face, 2400-3000 ft., 29 (13, UM; 7, USNM; 4, UA; 3, Carnegie; 2, BS); Catalina Mt. foothills, N face, 4200-4500 ft., 16 (15, UA; 1, UM); Oracle, 5000 ft., 18 (15, BS; 3, MVZ).

28. *Eutamias dorsalis dorsalis* (Baird).—Price (*op. cit.*) shot a

Gila or cliff chipmunk at 8000 feet elevation near snow in January. The preferred habitat seems to be wooded areas, but several have been taken below the oaks.

Total, 55: Pima Canyon, 3500 ft., 2 (BS); 9½ m. N, 3 m. E Tucson Court House, 4000 ft., 1 (UA); Oracle, 2 (BS); 8 m. SE Oracle, 3 (UM); 10 m. N, 17 m. E Pima Co. Courthouse, Tucson, 1 (UA); Santa Catalina Mts., 5100 ft., 1 (UA); near Soldier Camp, 7 (5, Carnegie; 2, MVZ); Summerhaven, 19 (BS, UM, UA, SDSNH); Santa Catalina Mts., 3 (USNM); Mt. Lemmon, 8800 ft., 2 (UA).

29. *Sciurus aberti aberti* Woodhouse.—The Arizona Game and Fish Commission released 31 males and 27 females in the Catalina Mountains in 1940 and 1941. The preferred habitat of the Abert squirrel is the ponderosa pine forest; sight records place their upper and lower limits in the fir and pinyon-juniper, respectively. Hunt data from the Arizona Game and Fish Commission for the Catalina Mountains reveals that 49 hunters bagged 105 Abert squirrels in 1953 and 23 hunters bagged 45 squirrels in 1955. (Information supporting recommendations to the Commission on 1956 hunting seasons).

Total, 7: 30 m. E Tucson on Mt. Lemmon Rd., 1 (UA); Mt. Lemmon Rd., 3 (UA); Rose Canyon, 5 m. above dam site, 1 (UA); Mt. Lemmon area, 7000 ft., 1 (UA); Marshall Saddle, 1 (UA).

30. *Sciurus arizonensis catalinae* Doult.—Doult (1931: 271) described *S. a. catalinae* from the Santa Catalina and Santa Rita mountains. The series consisted of one adult male and four adult females taken near Soldier Camp between August 17 and 30, 1927. These squirrels were feeding on white pine cones. Mearns (1907) reported them to feed on pine cone seeds, walnuts, acorns, berries, and green vegetation in the deciduous trees of canyons and streams at lower elevations. Price thought that they were "... probably found all through the lower pine zone, usually not overlapping the range of *S. aberti*." (in Allen, 1895: 245). Dice and Blossom (1937: 24) noted a few Arizona gray squirrels in the higher elevations. The rapid spread of the Abert squirrel in the Catalinas since its 1940 introduction may have acted adversely on an already small population of Arizona grays. The author knows of no reliable records of *S. a. catalinae* in the Catalinas in recent years.

Total, 14: Summerhaven, 6 (2, UM; 2, SDSNH; 1, UA; 1, BS); east side Santa Catalina Mts., 1 (USNM); near Soldier Camp, 8000 ft., 5 (Carnegie); Carter Canyon, 8000 ft., 1 (SDSNH); Mt. Bigelow, 8000 ft., 1 (MVZ).

31. *Thomomys bottae modicus* Goldman.—In a discussion of *Thomomys* in southeastern Arizona, Lange (1958) noted that: "... *Thomomys bottae* shows considerable variation that appears to be correlated with elevation. In general, gophers from the desert valley floors, such as those occurring in the lowlands along the Santa Cruz and San Pedro Rivers, are large and light-colored. Gophers from the pine forests on the mountain tops, such as those from the Santa Catalina and Rincon Mountains, are smaller and dark-colored.

Specimens from the pine belt of the Santa Catalina Mountains are . . . referred to *Thomomys bottae catalinae*. Specimens from the Santa Cruz River Valley are referred to *T. b. modicus*. The pocket gophers from Molino Basin . . . and from Reddington Pass . . . exhibit a combination of characters that appears to be a more or less random mixture of features of the adjacent lowland form, *T. b. modicus*, and adjacent pine zone forms, *T. b. catalinae* and *T. b. hueyi*. Although this morphological intermediate form has been named (as *T. b. parvulus* by Goldman, 1947: 26) additional specimens not available to the original describer have demonstrated that the supposed diagnostic characteristics do not exist. The small size supposed to be diagnostic of these gophers was evident in the specimens available to Goldman but further collecting at the type locality (Reddington Pass) revealed that all specimens available to Goldman were either juveniles, subadults, or young adults." These intergrades are referred to *T. b. modicus*.

Total, 34: Univ. Ariz. Agric. Exp. Farm, 5 (UA); Tucson, 2 (UA); 3 m. N Tucson, Oracle Rd., 2 (UA); 5 m. NW Univ. Ariz. Agric. Exp. Farm, 1 (UA); 5 m. N Santa Cruz R. bottoms, 1 (UA); Canada del Oro, 16 m. N Tucson, 3 (UA); Sabino Canyon, 12 m. NE Tucson, 3000 ft., 4 (UA); 10 m. N, 17 m. E Pima Co. Courthouse, 1 (UA); Santa Catalina Mts., S slope, Molino Basin, 4200 ft., 10 (intergrades) (KU); Reddington Pass, 12 m. E Tanque Verde Rd., 5 (intergrades) (UA).

32. *Thomomys bottae catalinae* Goldman.—Total, 12: Summerhaven and Mt. Lemmon area (UA).

33. *Perognathus flavus flavus* Baird.—The silky pocket mouse is known only from Ft. Lowell. "Mr. Miller found it not uncommon in the sandy fields around Fort Lowell." (Price, in Allen, 1895: 215). Dice and Blossom (1937: 26) trapped one in 1930 among cottonwoods and willows and regarded it as probably rare in the Tucson area. Total, 7: Ft. Lowell (4, USNM; 2, BS; 1, UM).

34. *Perognathus amplus taylori* Goldman.—L. H. Miller took one in sandy soil at Fort Lowell in 1894 (Allen, 1895). Dice and Blossom (1937: 26) found the Arizona pocket mouse most common on the sandy desert soils; none were collected above 4000 feet elevation. They trapped three animals eight miles north of Tucson in sand and small gravel and in palo-verde and brittle-bush, and trapped two others nine miles north of Tucson on gravelly and rocky slopes.

Total, 9: Ft. Lowell, 1 (USNM); 8 m. NE Tucson, near Ft. Lowell, 3 (UM); 8 m. N Tucson, 2700 ft., 3 (UM); 9 m. N Tucson, 2 (UM).

35. *Perognathus penicillatus pricei* J. A. Allen.—Dice and Blossom (1936: 27) found the desert pocket mouse in sandy and gravelly soils.

Total, 62: Ft. Lowell, 39 (BS); near Ft. Lowell, 13 (UM); 8 m. N Tucson, 6 (UM); 9 m. N Tucson, 2 (UM); 10 m. N Tucson, 2 (UM).

36. *Perognathus intermedius intermedius* Merriam.—Price re-

ported: "This is the common Pocket-mouse of the region south of the Mogollon Mesa, where it outnumbers all the others, three to one. We found it especially abundant at Fort Lowell . . . but as none were obtained at Fort Lowell in January, it is not unlikely that it hibernates during the colder months." (in Allen, 1895: 218-19). Dice and Blossom (1937: 28) also attest to its abundance: ". . . probably the most abundant mammal in the deserts of southern Arizona and northern Sonora." It has been taken on the north face in rocky habitat: three miles southeast of Oracle in open encinal, and in Peppersauce Canyon among ocotillo (Dice and Blossom, 1937: 29).

Total, 78: Ft. Lowell, 46 (USNM); 8 m. N Tucson, 1 (UM); 9 m. N Tucson, mouth Pima Canyon, 18 (UM); 10 m. N Tucson, 9 (UM); 3 m. SE Oracle, 4500 ft., 1 (UM); 8 m. SE Oracle, 4700 ft., 3 (UM).

37. *Perognathus baileyi baileyi* Merriam.—Dice and Blossom (1937: 26) recorded the Bailey pocket mouse as numerous on the rocky bahadas, but rare on the sandy desert soils. It has been taken in grassland on the north face at 4700 feet elevation.

Total, 57: near Ft. Lowell, 6 (UM); Santa Catalina Mt. foothills, S face, 32 (25, UM; 5, UA; 1, BS; 1, Carnegie); Oracle, 1 (BS); 2½-10 m. SE Oracle, 4400-4700 ft., 18 (13, UM; 5, UA).

38. *Dipodomys spectabilis* ssp.—Bannertail kangaroo rats are not common in the study area. Their mounds seem to be most numerous in the foothill country west and north of the mountains. Gibbs (1955) trapped an immature male among a group of mounds a few miles east of the Oracle junction.

Total, 8: 10 m. N Tucson, 2800 ft., 1 (BS); Oracle, 6 (BS); 1 m. S Oracle, 1 (UA).

39. *Dipodomys merriami merriami* Mearns.—This is the common kangaroo rat in the lower desert, ranging from the shrubby flats to the grasslands. Douthett (1934: 263) found the nocturnally active Merriam kangaroo rat in the same habitats as the diurnally active Harris ground squirrel.

Total, 73: Ft. Lowell, 25 (USNM); Santa Catalina Mt. foothills, S face, 2400-3000 ft., 43 (35, UA; 4, Carnegie; 3, KU; 1, UM); 3 m. S, 4 m. W Oracle, 1 (UA); 1 m. S Oracle, 4500 ft., 2 (UA); 6 m. ESE Oracle, 2 (UA).

40. *Dipodomys ordii ordii* Woodhouse.—Setzer (1949: 532) reports three Ord kangaroo rats collected at Fort Lowell. Dice took one in catclaws and mesquites (*Acacia* and *Prosopis*) southeast of Oracle (Dice and Blossom, 1937: 31).

Total, 8: Ft. Lowell, 3 (D.R.D.); Oracle, 4 (BS); 6 m. SE Oracle, 1 (UM).

41. *Castor canadensis* ssp.—Beaver were apparently introduced in Upper Sabino Canyon, Marshall Gulch, 7600 feet, in the early 1930's. There may have been later introductions. The following is an extract from the journal of D. J. T. Marshall, dated May 19, 1951: "Marshall Gulch, Catalina Mts., Arizona. At 10 AM starting down Sabino Canyon following creek . . . Beaver sign incr. got fresher

all way until into fresh droppings, dams, houses, cut willow twigs, cut greenery of white fir to plug dams, etc. — this about 4 or 5 miles down." Jackson (1954: 3) notes: "Streams found to contain beavers include . . . Sabino Canyon Creek . . . None of the areas were found to contain appreciable numbers of beavers." The author knows of no reliable records of beaver in the Catalinas in recent years.

42. *Onychomys torridus torridus* (Coues).—The southern grasshopper mouse has been taken in mesquite-grassland (Dice and Blossom, 1937: 32) and in desert shrub habitats. "This form appears to be abundant south of the Mogollon Mesa wherever there are sandy mesquite covered plains and river-bottoms. We found it abundant at Fort Lowell." (Price, in Allen, 1895: 225).

Total, 28: Ft. Lowell, 14 (USNM); Santa Catalina Mt. foothills, S face, 2400-2700 ft., 3 (UA); 2 m. E Oracle jct., Pinal Co., 4 (UA); Oracle, 4 (3, BS; 1, UM); 3 m. E Oracle, 1 (UA); 6 m. SE Oracle, 4400 ft., 2, (UA).

43. *Reithrodontomys megalotis megalotis* (Baird).—The western harvest mouse is represented by only one specimen, taken in 1923. Dice, in 1932, secured a specimen five miles north of Oracle in palo-verde, mesquite, and grass (Dice and Blossom, 1937: 32).

Total, 1: 2 m. E Ft. Lowell (BS).

44. *Peromyscus maniculatus sonoriensis* (Le Conte).—This lowlands form has been collected in grassy areas on both sides of the mountains. It has been taken in the same trap-line with *P. eremicus* and *P. boylei* at Molino Basin on the south face of the mountains. This area along the Mt. Lemmon highway is in the Upper Desert Slopes zone of Shreve (1915). The vegetation consists of scattered oaks and mesquites; ocotillos and agaves; shrubs, mainly *Aplopappus*, *Baccharis* and *Asclepias*; and grasses. The ground cover, which is much more extensive than in the bahadas; is broken along the creek by rocks and boulders. At 4200 feet, this area represents the lower limits of *P. boylei* and the upper limits of *P. eremicus*. *P. m. sonoriensis* and the following subspecies are apparently separated by the oak and pinyon-juniper vegetation.

Total, 7: Molino Basin, 4200 ft., 3 (UA); Oracle, 2 (BS); Linda Vista Ranch, 2½ m. S Oracle, 1 (UA); 10 m. SE Oracle, Pinal Co., 4600 ft., 1 (UM).

45. *Peromyscus maniculatus rufinus* (Merriam).—The tawny deer mouse is common in the higher elevations. Dice and Blossom (1937: 34) found them more common in the Douglas firs than in the ponderosa pine.

Total, 74: Summerhaven, 7500-7600 ft., 27 (25, UM; 2, BS); Carter Canyon, 7600 ft., 1 (UA); Soldier Camp, 7 (6, Carnegie; 1, MVZ); N slope Mt. Lemmon, 8000-8600 ft., 38 (UM); N slope Mt. Lemmon, 8800 ft., 1 (UA).

46. *Peromyscus boylei rowleyi* (J. A. Allen).—Doutt (1934: 265) and Dice and Blossom (1937: 35) noted the brush mouse in wooded areas from the lower oaks to the firs. Dice and Blossom

(1937: 36) found it most abundant in the encinal, and thought that this was related to the animal's semi-arboreal nature.

Total, 98: Santa Catalina Mts., 8 (BS); Molino Basin, 4200 ft., 20 (10, UA; 10, KU); Oracle, 1 (BS); 1½ m. S Oracle, 4500 ft., 2 (UA); 5-8 m. SE Oracle, Pinal Co., 26 (13, UA; 7, UM; 6, MVZ); Santa Catalina Mts., rocky hillside, 5200 ft., 2 (UA); Santa Catalina Mts., N base, 5500 ft., 1 (BS); Santa Catalina Mts., N slope, 5600 ft., 2 (UM); near Soldier Camp, 3 (Carnegie); Summerhaven, 34 (31, UM; 2, UA; 1, BS); Mt. Lemmon, N slope, 8550 ft., 1 (UM).

47. *Peromyscus eremicus eremicus* (Baird).—The cactus mouse ranges from the lowest limits of the study area to about 4300 feet on the south face and 4700 feet on the north face.

Total, 111: Ft. Lowell, 15 (8, UM; 4, BS; 3, USNM); Santa Catalina Mt. foothills, S face, 24-3000 ft., 45 (32, UA; 12, UM; 1, KU); Upper Sabino Canyon, 3200 ft., 4 (UA); Finger Rock Canyon, 3200 ft., 1 (UA); Pima Canyon, 3500 ft., 2 (BS); 3 m. N, ½ m. E Redington, 2 (UA); 2 m. S, 1½ m. W Redington, 4000 ft., 10 (UA); Molino Basin, 4200 ft., 7 (UA); 1 m. W, 1 m. S Oracle, 1 (UA); Linda Vista Ranch, 2½ m. S Oracle, 1 (UA); 6-8 m. SE Oracle, Pinal Co., 23 (21, UM; 2, UA).

48. *Peromyscus leucopus arizonae* (J. A. Allen).—This form has been taken on both sides of the Catalinas, but apparently is rare.

Total, 4: Ft. Lowell, 2 (1, BS; 1, USNM); 4¾ m. S, 3 m. E Oracle, Pinal Co., 4600 ft., 2 (UA).

49. *Sigmodon hispidus cienegae* A. B. Howell.—The type locality of *Sigmodon hispidus cienegae* is Bullock's Ranch, four miles east of Fort Lowell (Miller and Kellogg, 1955: 525). The hispid cotton rat has been collected in the following localities: along Rillito Wash; Binghampton pond; a cattail (*Typha*) marsh in Lower Sabino Canyon; in grass along a fence row at the University of Arizona Farm; and along a dry wash in *Prosopis* and *Opuntia* growth.

Total, 12: Ft. Lowell, Rillito Wash, 2 (UM); Binghampton pond, 7 m. NE Tucson, 4 (3, UA; 1, MVZ); Univ. Ariz. Farm, 1 (UA); Lower Sabino Canyon, 3 (UA); 20 m. N Tucson, Pinal Co., 1 (UA); 2 m. E Oracle jct., 1 (UA).

50. *Neotoma albigula albigula* Hartley.—The type locality of *Neotoma albigula albigula* is in the vicinity of Fort Lowell (Miller and Kellogg, 1955: 535). Price found the white-throated woodrat abundant by Fort Lowell, "... having numerous nests among cactus beds, brush fences, and in willows along the Rillito." (in Allen, 1895: 223). It is common in the grasslands of the north face (Dice and Blossom, 1937: 38). None have been taken in ponderosa pine, but one has been collected in encinal on the north face.

Total, 91: Ft. Lowell, 12 (6, MVZ; 4, BS; 2, USNM); near Ft. Lowell, 17 (11, MVZ; 5, BS; 1, UM); Santa Catalina Mt. foothills, S face, 2400-3000 ft., 13 (9, UA; 2, UM; 2, KU); Pima Canyon, 3500 ft., 3 (BS); Redington Pass, 24 m. E Tucson, 1 (UA); near Redington, 2 (UA); Molino Basin, 4200 ft., 7 (UA); Oracle, 6 (5, BS; 1, SDSNH); 1½-2½ m. SW

Oracle, 3 (UA); 3-10 m. SE Oracle, Pinal Co., 26 (UM); Santa Catalina Mts., N base, 5500 ft., 1 (BS).

51. *Neotoma mexicana bullata* Merriam.—This race of the Mexican woodrat is known only from the Catalina Mountains, where it is confined to the higher elevations. Dice found nests around boulders on ponderosa pine slopes and noted one animal in oak brush near Summerhaven (Dice and Blossom, 1937: 39).

Total, 20: Summerhaven, 16 (7, UM; 5, BS; 3, UA; 1, SDSNH); Carter Canyon, 3 (UA);  $\frac{1}{2}$  m. SE Soldier Camp, 7900 ft., 1 (Carnegie).

52. *Mus musculus* ssp. Total, 4: near Ft. Lowell, 3 (2, BS; 1, UM); Molino Basin, 4200 ft., 1 (UA).

53. *Rattus norvegicus norvegicus* (Berkenhout).—Total, 1: Ft. Lowell (USNM).

54. *Erethizon dorsatum couesi* Mearns.—Porcupines have been seen near Rillito Wash on Sabino Canyon Road, in the Catalina foothills (near Campbell Avenue and East River Road), and in Upper Sabino Canyon (about 3200 feet). The observations and comments of Reynolds (1957) are of interest here. Taylor's finding (1935: 103) that pinyon pine is apparently relished by porcupines may indicate that *Erethizon* spends considerable time in this vegetative type. Other records are as follows: a road-kill on the Mt. Lemmon highway two miles above the prison, and a specimen taken on the north face just below the top by predator control agents. Indications are that *E. d. couesi* has a wide tolerance and adaptability in the Catalinas.

55. *Euarctos americanus amblyceps* (Baird).—Vernon Bailey (1889) reported bear tracks "near the summit and along the streams." The *Arizona Daily Star*, in 1898, reported that: "Ed Johnson and family, who have been camped on Mt. Lemmon for some time, have been heard from . . . it is reported they have killed ten bears, eight mountain lions, 17 wolves. . . ." A few black bears still inhabit the higher elevations. Gerald I. Day reported a July 1956 sight record by Harold Lim near Summerhaven. This bear was observed at night in a refuse area. Boy scouts at Camp Lawton, Mt. Lemmon, made a cast of a black bear track near Summerhaven in July 1956 (L. R. Commissaris, personal communication). Forest Service personnel have sighted black bear in the Catalinas, but not in recent years.

56. *Procyon lotor mexicanus* Baird.—Price (in Allen, 1895: 250) said this of the raccoon: ". . . common in willow thickets along the Rillito Creek at Fort Lowell." Sight records and reports indicate that *P. l. mexicanus* is most common in picnic and resort areas, particularly Sabino Canyon and Summerhaven. These areas are located near streams, where the raccoon may secure water and additional food.

Total, 4: Ft. Lowell, 2 (USNM); Sabino Canyon, 1 (BS); Summerhaven, 1 (UM).

57. *Nasua narica molaris* Merriam.—The coati-mundi is herein reported from the Santa Catalina Mountains for the first time on the basis of the following records: (1) William J. Schaldach, Jr., reported sighting one in the ponderosa pines near Summerhaven and six in Upper Sabino Basin in 1945; and (2) C. Roger Hungerford reported *Nasua* tracks in a dry wash near the Old Desert School, about ten miles north of Tucson, in *Simmondsia-Carnegie* habitat, in 1956. Coati-mundis have now been reported from the following mountain ranges in southeastern Arizona: Santa Catalinas, Huachucas, Chiricahuas, Patagonias, Santa Ritas, and Tumacacoris (Taber, 1940: 13).

58. *Bassariscus astutus arizonensis* Goldman.—Ringtail cats range from the lowest to the highest limits of the study area. Like raccoons, they seem to be most common in picnic and resort areas, particularly those with streams flanked by rocky hillsides. Summerhaven residents report them coming into their attics. Ringtails undoubtedly range at times from Summerhaven and Soldier Camp into the firs at higher elevations.

Total, 5: edge of Tucson, 1 (UA); 16 m. E Tucson on Tanque Verde Rd., 1 (UA); Ft. Lowell, 3 (A. B. Howell).

59. *Spilogale putorius leucoparia* Merriam.—This species and the three reported below are probably sympatric at the lower elevations of Sabino Canyon. The following records from Sabino Canyon are the author's: sight and specimen records for *Spilogale*; sight, and trap and release records for *Mephitis mephitis*; and sight records for *Conepatus*. In addition, *Mephitis macroura* has been taken at Fort Lowell and probably inhabits the lower elevations of Sabino Canyon as well. The relationships of this distributional pattern would be an interesting and revealing study.

Total, 10: Ft. Lowell, 1 (USNM); Lower Sabino Canyon, 2 (UA); Sabino Canyon, 1 (USNM); Molino Basin, 20 m. NE Tucson, 1 (UA); Stratton Mine, Santa Catalina Mts., 1 (Carnegie); near Soldier Camp, 4 (Carnegie).

60. *Mephitis mephitis estor* Merriam.—Total, 7: Ft. Lowell, 3 (USNM); near Soldier Camp, 2 (Carnegie); near Summerhaven, 1 (UA); Carter Canyon, 7600 ft., 1 (UA).

61. *Mephitis macroura milleri* Mearns.—The hooded skunk has been collected in the study area only at the type locality, Fort Lowell. Total, 3: Ft. Lowell (2, MVZ; 1, BS).

62. *Conepatus mesoleucus venaticus* Goldman.—Collection and sight records are from the lower elevations. Dice and Blossom (1937: 19) report forest ranger observations at the higher elevations. Total, 3: Vicinity of Ft. Lowell, 1 (MVZ); mouth Sabino Canyon, 6 m. N, 10 m. E Tucson, 1 (KU); Sabino Canyon, 17 m. NE Tucson, 1 (UA).

63. *Taxidea taxus berlandieri* Baird.—Price regarded the badger as common in the plains region (in Allen, 1895). The author has

seen a badger in gravelly soil at 4200 feet elevation on the north face just below Reddington Pass in the following vegetation: scattered mesquites, acacias, oaks, ocotillos, *Aplopappus*, and grasses.

Total, 3: Ft. Lowell, 2 (1, BS; 1, Stanford); Peppersauce Canyon, 1 (Carnegie).

64. *Vulpes macrotis arsipus* Elliot.—The following is part of a letter from C. E. Gillham to W. P. Taylor, dated April 19, 1934: "As far as I know from personal trapping and observation of other trappers, the swift fox is found to some extent in practically all the desert areas, probably from the San Pedro River west and on into California in the sand dune country . . . and they are found to some extent on practically all the desert range south, you might say, of the oak country in what would be usually the true desert type of Arizona. It seems to me one usually finds swift fox most abundant where the nature of the desert is sandy rather than rocky. Probably either his own burrowing tendencies or the desire for burrowing for rodents may have something to do with this." Records from the Catalinas confirm Gillham's observations: the swift fox is most common in the shrubby desert flats and the foothill country. Trapping and poisoning campaigns have greatly reduced their numbers.

65. *Urocyon cinereoargenteus scottii* Mearns.—The gray fox seems to be most common in the foothills and canyon mouths, but it also occurs in the pines and firs. Taylor (1924) found *Juniperus pachyphloea* fruits almost exclusively in gray fox droppings collected in Sabino Canyon below the Basin. Dice and Blossom (1937: 19) noted what were probably gray fox feces on a ponderosa pine slope. These droppings contained rock squirrel and woodrat hair. The diet may vary with the habitat and with the season.

Total, 14: Ft. Lowell, 8 (A. B. Howell); Tanque Verde, 1 (KU); Santa Catalina Mts., 4 (BS); mouth Sabino Canyon, 6 m. N, 10 m. E Tucson, 1 (KU).

66. *Canis latrans mearnsi* Merriam.—Coyotes have been heard in Peppersauce Canyon, about eight miles southeast of Oracle (Dice and Blossom, 1937: 20), and at Summerhaven. Their preferred habitat or area of greatest concentration may be in the lower elevations.

Total, 3: Santa Catalina Mts., 1 (Carnegie); Ft. Lowell, 1 (DRD); 25 m. N Tucson, 1 (Carnegie).

67. *Canis lupus baileyi* Mearns.—The *Arizona Daily Star*, in 1898, reported that: "Ed Johnson and family, who have been camped on Mt. Lemmon for some time, have been heard from . . . it is reported they have killed . . . 17 wolves. . . ." The following is an extract of a letter, dated November 28, 1956, from Everett M. Mercer to the author: "During April of 1937, I spent three days hunting lions . . . in the Santa Catalina Mountains. We saw the tracks of a large wolf during the second day that we were there, and we followed it for two

or three miles. It came out on top of the mountain and drifted off to the east toward the San Pedro River." A Pittman-Robertson hunter employed by the Game Department took a wolf in July, 1948, in the Catalinas (Mercer, 1949: 6). Pierre Early, a reliable observer, has reported the following to me, in a letter dated August 18, 1958: "About the Mex. Lobos. the first sight of them would have been in October 1955—one carrying uneaten portion of a large yearling whitetail. Second sighting about March or April 1956—the pair sighted near our dump grounds. Sign has been seen several times since." The locality is the mouth of Sabino Canyon, elevation 3000 feet.

68. *Felis concolor azteca* Merriam.—Mountain lions inhabit the higher elevations. Annual game population estimates for the Santa Catalina District, Coronado National Forest, run from 10 to 18 animals for the period, 1937 to 1948. Douth (1935) reports sight records near Soldier Camp. Dice and Blossom (1937: 20) report that one cougar was killed in 1932 near Soldier Camp. Mountain lion sign has been found in the Mt. Lemmon, Upper Sabino, and Stratton Mine areas (Knipe, 1951). Total, 1: Santa Catalina Mts., Pinal Co./UA).

69. *Lynx rufus baileyi* Merriam.—Bobcats, like most of the larger predators in the Catalinas, range from the desert flats to the pines and firs. The preferred habitat, if any, is not known. Annual game population estimates for the Santa Catalina District, Coronado National Forest, range from 400 to 550 animals for the period, 1937 to 1948. Total, 1: Ft. Lowell (BS).

70. *Tayassu tajacu sonoriensis* (Mearns).—Although javelina are most common in desert shrub habitat, such as *Simmondsia*, they have been seen in ponderosa pine at an elevation of 6700 feet (Reed, 1956) and in oak and ponderosa pine on the east side and in the Canada del Oro country (Knipe, 1953). Some indication of population size in the study area is given by the following hunt kills, gathered and compiled by personnel of the Arizona Game and Fish Department: 1952, 76; 1953, 88; 1954, 80; 1955, 138; and 1956, 90. Total, 1: Santa Catalina Mts. (MVZ).

71. *Odocoileus virginianus couesi* (Coues and Yarrow).—Coues deer range from the flats to the summits. The author has seen them in Lower Sabino Canyon, elevation 3000 feet, in September. They usually range above mule deer, however, and are most common in the higher elevations. Total, 3: Santa Catalina Mts., 1 (USNM); 2 m. SE Soldier Camp, 1 (Carnegie); Summerhaven, 1 (UM).

72. *Odocoileus hemionus crooki* (Mearns).—Mule deer range through the desert shrubs in the flats and foothills on the south face, and through the desert grasses and shrubs on the north face. Price (in Allen, 1895) found them in foothills and ravines of the lower mountain ranges and thought that they preferred open country with oak woods.

73. *Ovis canadensis mexicana* Merriam.—The Catalina bighorns have been mentioned by many writers, among them the following: "In the year 1885 I ascertained that mountain sheep occurred in the . . . Santa Catalina mountains. . . ." Mearns (1907: 239); "Not uncommon on the bare rocky spurs of the Santa Catalina Mountains, where they were seen during 1894. Several were killed in the fall of 1893 by an Indian hunter, and the meat sold to settlers at the foot of the mountains. . . ." Price (in Allen, 1895: 258); and Hornaday (1908: 341-42). Fred Winn, Coronado National Forest supervisor, stated in the *Tucson Citizen* (anonymous, 1928) that the most recent game census estimated 220 sheep in the Catalinas and that this population was the largest in the state. The 1937 census estimated 80 sheep from fresh sign and actual sightings (Bogar, 1956). Poaching, drought, and the development of roads caused continual decline in the Catalina bighorn population (Bogar, 1956). Knipe (1951) saw six animals and estimated the number at 35; Reed (1956) thought that the maximum number was 15, with the probable number between six and ten.

Total, 2 (3?): Santa Catalina Mts., 1 (UA); near Old Sutherland Ranch, Canada del Oro, 1 (BS); Santa Catalina Mts. or some near-by range, 1 (BS).

#### HYPOTHETICAL AND EXTINCT SPECIES

1. *Sylvilagus floridanus holzneri* (Mearns).—This species generally ranges from the lower encinal into the ponderosa pines in those mountains of southern Arizona where it has been found (Sowls, 1957: 235). Local residents have reported a large cottontail from the Catalinas (Dice and Blossom, 1937: 43); it seems likely that this form is found in the oaks and pines of the Catalinas.

2. *Ursus* sp. (*U. arctos* L. ?).—It seems likely that grizzlies formerly occurred in the Catalinas, but their date of extinction is not known. The only references appear to be the following: (1) Vernon Bailey (1889): "The grizzly is here called the Silver-tip Bear. They are said to be common. I saw a number of bear tracks high up in the mts. and one very large track that must have been made by a Grizzly. Other smaller tracks were probably of Black or Brown Bears. Most of the tracks were near the summit and along the streams." (2) M. E. Musgrave, in a letter dated June 7, 1921: "We also have another grizzly that ranges in the Rincon Mountains, north of Tucson."

3. *Felis yaguarondi tolteca* Thomas.—Little (1938) reports sighting a jaguarundi in Santa Cruz County, Arizona, on March 17, 1938. This appears to be the only record of this subspecies in the United States up to the present time, with the following possible exceptions. Peterson and Fisher (1955: 236) record this observation along the Sabino Canyon Road: ". . . a black cat padded across bone-dry Pantano Wash . . . the black form of the jaguarundi. . . . We had the privilege of glimpsing this little-known cat in a part of its range where

it is very rare." The author has a sight record of "a stocky, long-tailed, cat-like animal" in Upper Sabino Canyon, 3200 feet, on November 16, 1956, but in consideration of the brevity of observation and the rarity of the animal involved, he mentions it merely for possible future significance.

4. *Felis onca arizonensis* Goldman.—Nelson and Goldman (1933: 237) give the range of this subspecies of the jaguar as the mountainous regions of eastern Arizona, southwestern New Mexico, and northeastern Sonora, Mexico. Jaguars occasionally passed through the Catalinas and apparently still occur in southern Arizona. Herbert Brown (*in* Hock, 1955: 325) referred to a jaguar-kill in the Rincon Mountains in 1902. C. T. Vorhies (*in* Seton, 1929: 11) reported that one was taken in the Catalinas around 1912, and one was killed in the adjacent Rincon Mountains in 1912. E. A. Goldman saw the skin of a jaguar taken in the Tortolito Mountains, about 30 miles northwest of Tucson, in 1913. The Holbrook *Observer* of January 20, 1920, reported a jaguar killed in the Rincon Mountains, Pima County, "on Saturday." One was seen in September, 1920, about three miles northwest of Tucson in Pima County along the Silverbell Highway. The animal was traveling east, towards the Santa Catalina Mountains (Vorhies, *in* Seton, 1929: 10). E. A. Goldman, in memorandums dated July 17-18 and August 4-9, 1923 reported that: "A man named Al James is said to have seen a jaguar that killed one of his burrows near Mt. Lemmon about July 1st."

5. *Felis pardalis sonoriensis* Goldman.—Goldman (1943: 378) gives the range of the subspecies *sonoriensis* as the west slopes of the Sierra Madre, northward from southern Sonora to southeastern Arizona, formerly west to Fort Verde in Yavapai County, Arizona. It is possible that ocelots formerly passed through the Catalinas.

6. *Antilocapra americana* ssp.—The pronghorn antelope was known from the study area until some 30 years ago. The following records are pertinent: (1) W. P. Taylor (1925), referring to the Oracle Plains: "Stanley Kitt, a long time resident of Tucson, says he remembers seeing bands of 20 to 40 antelope. . . . This was in the 80's."; (2) Vernon Bailey (1889), referring to Oracle: "Said to be a few in the valley below here."; (3) A. K. Fisher (1892): "Mr. Herbert Brown saw a band of twenty or more near Tucson in the spring."; (4) E. A. Goldman (1923), referring to the road to Florence, 35 miles northwest of Tucson: "J. H. Durham, an old cattle man familiar with game conditions, reports having seen 5 antelope . . . in June of this year."

The following are included in the hypothetical list on the basis of their known distribution in Arizona:

7. *Sorex merriami leucogenys*, higher elevations(?)

8. *Mormoops megalophylla*, oaks (?)

9. *Leptonycteris nivalis*, oaks (?)
10. *Myotis occultus*
11. *Myotis evotis*
12. *Lasionycteris noctivigans*, higher elevations in summer (?)
13. *Tadarida molossa*
14. *Perognathus longimembrus*
15. *Perognathus hispidus*
16. *Reithrodontomys montanus*, grasslands on north face (?)
17. *Reithrodontomys fulvescens*
18. *Peromyscus merriami*, mesquite bosques and washes (?)
19. *Sigmodon minimus*, oaks (?)

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## The Genitalia of the Buffalo Treehopper, *Stictocephala bupalus* (Fabricius)

CLIFFORD J. DENNIS

*East Central State College, Ada, Oklahoma*

Genital morphology is often used as a basis of insect taxonomy. To be useful, a taxonomic character must be constant and unique. In theory, the genital structures should be constant within each species. The purpose of this study has been to determine the degree of constancy or variability in the genitalia of both sexes of the buffalo treehopper, *Stictocephala bupalus* (Fabricius).

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### PROCEDURE

Specimens of both sexes were secured from the greater part of the range of this species in North America. A total of 2021 specimens (consisting of 1009 males, 1009 females and 3 with features of both sexes) from 39 states, the District of Columbia and 7 Canadian provinces were examined.

The abdomens were cleared in 10 per cent potassium hydroxide solution, washed in water and stored in corked 10 x 25 mm vials in glycerine. The vials were pinned separately, and corresponding numbers were attached to the specimen pins and the vial pins. Examination and dissection were carried out under glycerine in a spot plate.

The terminology employed is that which I used in an earlier paper (Dennis, 1952).

#### GENERAL DESCRIPTION OF THE GENITALIA

##### MALE

The male parts are illustrated in Figures 1-6. The dorsal abdominal tergite IX, the lateral valves and the ventral subgenital plate enclose the aedeagus, the styles and the connective. Abdominal tergites X and XI form the anal tube.

The lateral valves each have a single broad, blunt tooth. The subgenital plate is broadly rounded at its base and narrowed in the distal half; the distal margin has a small acute notch.

The anterior arm of the aedeagus articulates with the base of the anal tube. Ventrally, the aedeagus is lobed at its articulation with the connective. The posterior arm of the aedeagus has lateral membranes which meet below the middle of its anterior face. In the middle of the posterior face of the posterior arm is the functional orifice which is rounded below, acute above and equals two-thirds of the height of the arm. The aedeagus is the penis sheath.

The connective is elliptical except for a shallow, rounded notch in its anterior margin. Its sides are folded dorsally so that it appears V- or U-shaped when viewed from the end.

The styles articulate laterally with the connective. The point of articulation of the styles and the connective is the dividing point between the anterior and posterior arms of these structures. The anterior arms are roughly cylindrical, divergent and with no distinctive features. The posterior arms are upturned distally, almost straight in dorsal aspect and acuminate at their tips. On the outer margin of each posterior arm is a row of short hairs on the distal two-thirds; the inner margin has a similar row on the distal half to third. The styles are used as claspers during copulation.

##### VARIATION IN THE MALE

*Abdominal tergites IX, X and XI*.—These structures exhibit no significant variation.

*Subgenital plate*.—The subgenital plates are also rather constant and have the form illustrated in Figure 2. One specimen from South Dakota has the posterior notch extended as a split reaching one-third of the way to the base (Fig. 7).

*Lateral valve*.—The valves themselves have practically no variability in form, but the teeth do show a few variations. The typical form of the tooth is shown in Figure 4. Most variations are very slight and of little significance. Nine specimens have teeth which are noticeably narrower than the typical form (Fig. 8). The narrow teeth were found on one specimen which was collected in Wisconsin, one from Washington, two from Ontario, two from Iowa and three from Michigan. A specimen from Wyoming has blunt teeth (Fig. 9).

Two treehoppers, one from Kansas and one from Oklahoma, have a slight ventral sinuation near the tip of the tooth (Fig. 10). One specimen from British Columbia has a narrow tooth on the left valve and a typical tooth on the right valve.

*Connective*.—No significant variations were found in the connectives; they all appear as is shown in Figure 3.

*Styles*.—The styles are rather constant, exhibiting only very slight variations. A typical style is illustrated in Figures 1 and 3. The only noticeable variation is a small dorsal notch at the tip of the right style of a single Maryland specimen (Fig. 11). A few styles appeared to be very slightly curved inward at the tips.

*Aedeagus*.—The anterior arm shows considerable variability; the posterior arm is much more constant in form but still has some slight variations. What is considered to be the typical form is illustrated in Figures 5 and 6.

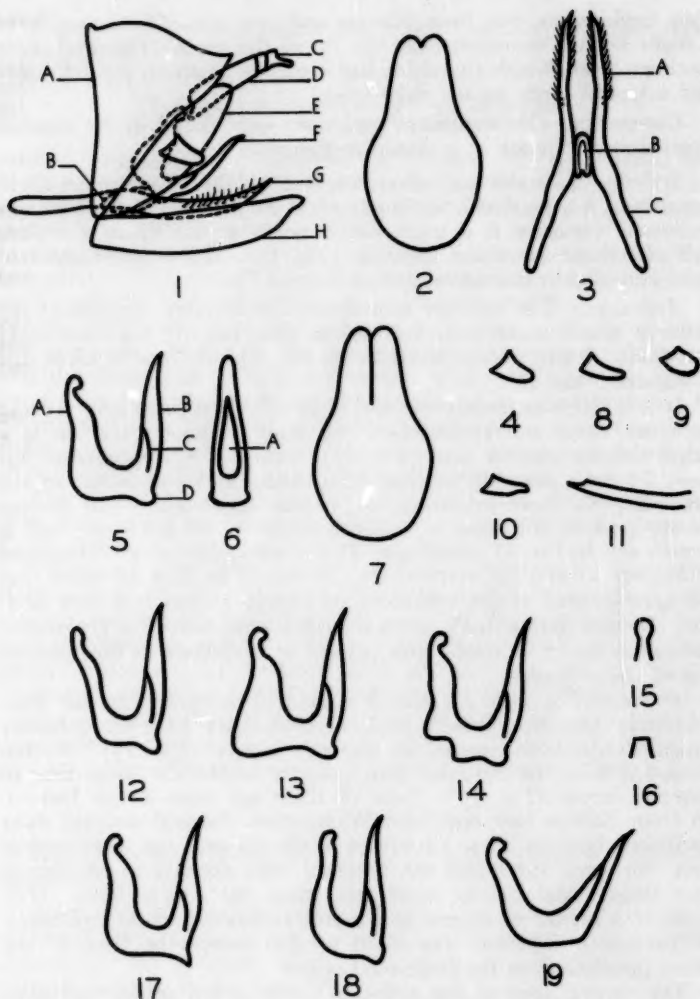
It is difficult to classify the variations of the anterior arm because there are many intergradations. The most common variation is a rather slender anterior arm (Fig. 12), found in 121 specimens. Of these, 71 have normally sclerotized genitalia and abdomens; in the remaining 50, these structures are weakly sclerotized. The antero-ventral part of this arm is rather bulbous in 33 specimens and is broadly notched in 35 specimens. These two variations are illustrated in Figures 13 and 14, respectively. It should be kept in mind that this arrangement of the variations into three groups is a very arbitrary one and that actually much intergradation exists. No geographic correlation could be made with respect to variations in the anterior arm of the aedeagus.

The posterior arm is rather constant. Ten specimens, six from Michigan, three from Alberta and one from Iowa, have the definitely expanded tip when viewed in posterior aspect (Fig. 15). Fifteen specimens have the posterior arm truncate at the tip when seen in posterior aspect (Fig. 16). Four of these are from South Dakota, ten from Kansas and one from Washington. Several aedeagi show gradations between these variations of the tip and the more typical form. In some specimens the posterior arm appears to be slightly more slender and slightly more erect than the typical form. This, again, is a matter of degree and is not considered to be significant. No particular variation was noted in the position or form of the lateral membranes or the functional orifice.

The ventral lobe of the aedeagus shows a few minor variations in form. The only striking variation is in two specimens, one from Iowa and one from Wyoming, which have an acute lobe when viewed from the side (Fig. 17).

One specimen from New York and one from Maryland have the two arms of the aedeagus closer together than usual (Fig. 18).

Two specimens, one from Wyoming and one from Michigan, have the anterior arm and the posterior arm distinctly more divergent than usual (Fig. 19).



Figs. 1-19. Male genitalia. 1. Terminalia, left lateral view; A, Tergite IX; B. Connective; C. Tergite XI; D. Tergite X; E. Lateral valve; F. Aedeagus; G. Style; H. Subgenital plate. 2. Subgenital plate, ventral, posterior margin up. 3. Styles and connective, dorsal; A. Style, posterior arm; B. Connective; C. Style, anterior arm. 4. Tooth of lateral valve, usual form. 5. Aedeagus, lateral; A. Anterior arm; B. Posterior arm; C. Lateral membrane; D. Ventral lobe. 6. Aedeagus, posterior; A. Functional orifice. 7. Subgenital plate, South Dakota specimen. 8-10. Tooth of lateral valve. 8. Narrow form. 9. Wyoming specimen.

## FEMALE

Figures 20-23 illustrate the female parts. Abdominal tergite IX, sternite VII and valvulae 1 and 3 enclose valvula 2 and the valvifers. The anal tube is composed of tergites X and XI.

Sternite VII is truncate basally and slightly rounded on the sides. Its posterior margin is a subacute-bottomed notch with broadly sinuate sides reaching half the depth of the sternite.

The two valvulae 1 have the tips narrowed, sinuate above and below, with transverse ridges extending below the ventral margin. The one valvula 2 typically has a single tooth somewhat removed from the coarse dorsal serrations before the tip. Valvula 2 is closed dorsally to the single tooth, open from the single tooth to the tip and ventrally. The base of valvula 2 is bifurcate with the arms curving upward. The two valvulae 3 are narrow in the basal half and then rather abruptly broadened dorsally and tapered to the rounded tip; the broadened part is somewhat spoonshaped.

Near the bases of the inner aspect of tergite IX are condyles which articulate with the two second valvifers. These valvifers articulate posteriorly with valvulae 3 and anteriorly with the arms at the base of valvula 2. The two first valvifers join the bases of valvulae 1. Valvulae 1 and laterally connected with valvula 2 by tongue-and-groove sliding joints.

Valvula 2 is the ovipositor proper. It slides on valvulae 1 in a saw-like motion as the eggs are inserted under the bark of twigs. The dorsal teeth before the tip aid in cutting bark.

## VARIATION IN THE FEMALE

*Abdominal tergites IX, X and XI*.—These tergites show no significant variation.

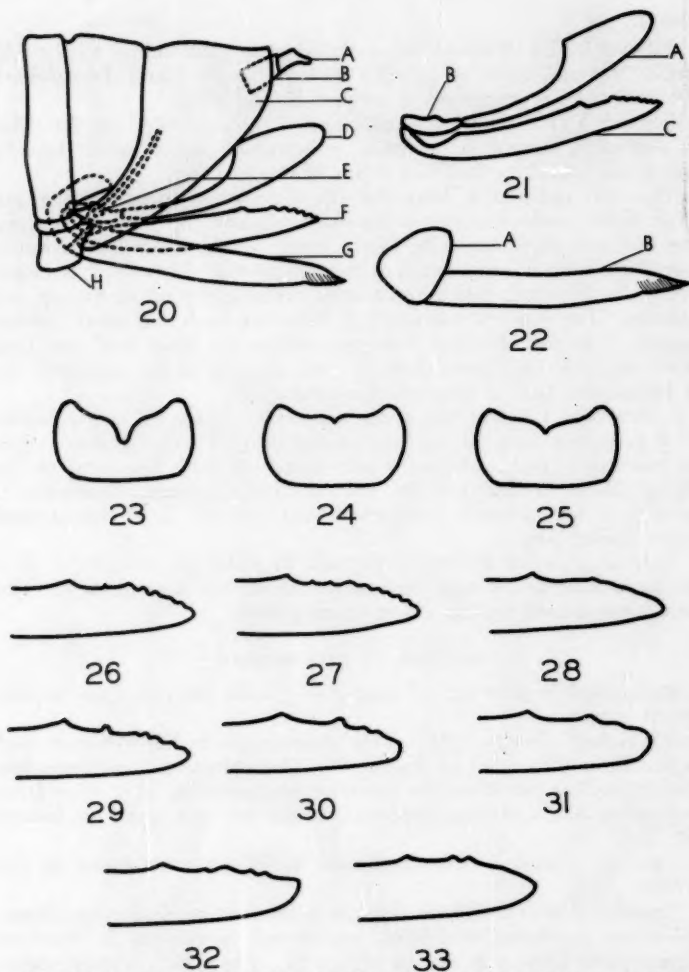
*Abdominal sternite VII*.—This structure is rather constant and has the form illustrated in Figure 23. One Maryland specimen has a rather shallow notch on the posterior margin (Fig. 24). One from Washington has a similar posterior margin, but not quite as shallow (Fig. 25).

*Valvifers 1 and 2*.—No significant variations were found in the valvifers.

*Valvulae 1 and 3*.—These valvulae exhibit no particular variations.

*Valvula 2*.—Some variability was found in valvula 2. The tip of the typical form is shown in Figure 21. The most common variation is the presence of a tiny tooth between the single tooth and the coarse serrations (Fig. 26). This was found on 58 females collected throughout the range of this species. The position of this tiny tooth

10. Kansas and Oklahoma specimens. 11. Style, right lateral, Maryland specimens. 12-19. Aedeagus. 12. Lateral, slender anterior arm. 13. Lateral, bulbous antero-ventral part. 14. Lateral, broadly notched antero-ventral part. 15. Tip, posterior, expanded. 16. Tip, posterior, truncate. 17. Lateral, acute ventral lobe. 18. Lateral, arms close together. 19. Lateral, arms divergent.



Figs. 20-33.—Female genitalia. 20. Terminalia, left lateral view; A. Tergite XI; B. Tergite X; C. Tergite IX; D. Valvula 3; E. Condyle; F. Valvula 2; G. Valvula 1; H. Sternite VII. 21. Valvulae 2, 3, valvifer 2, left lateral; A. Valvula 3; B. Valvifer 2; C. Valvula 2. 22. Valvula 1, valvifer 1, left lateral; A. Valvifer 1; B. Valvula 1. 23-25. Sternite VII, ventral, posterior margin up. 23. Usual form. 24. Maryland specimen. 25. Washington specimen. 26-33. Valvula 2, variations of tip, left lateral. 26. Tiny tooth between single tooth and serrations. 27. Two tiny teeth between single tooth and serrations. 28. Obscure serrations. 29. Colorado specimen. 30. Pennsylvania specimen. 31. Indiana specimen. 32. Wisconsin specimen. 33. Massachusetts specimen.

is not uniform; it was found at various positions between the single tooth and the serrations. Four specimens, one from New Jersey, one from Kansas and two from Nebraska, have two tiny teeth between the single tooth and the serrations (Fig. 27).

Rather obscure serrations are present on 16 specimens from widely scattered localities (Fig. 28). Four of these from Iowa also have weakly sclerotized abdomens. Five other variations in tips which occurred on single specimens from Colorado, Pennsylvania, Indiana, Wisconsin and Massachusetts are shown in Figures 29-33.

The number of teeth in the serrations varies from three to nine, with the usual number being from six to eight.

The tip of valvula 2 exhibits some slight variations in form, but this is of little consequence. Some are slightly more blunt than the typical form; others are somewhat more narrowed.

#### DISTORTIONS

##### MALES

1. This specimen is in the collection of Iowa State University. Label data: (illegible word), New Mexico; 9,21,88. All parts of this insect are normal except the anterior arms of the styles which are half normal length and the anterior arm of the aedeagus which also is reduced. The aedeagus is illustrated in Figures 34 and 35.

2. The Iowa State University collection also contains this specimen. Label data: Boone, Iowa; 20 July, 1916; Collector L. S. Wells. This is again a normal-appearing insect in all respects except for the left style which is rather short and thick and has a dorso-lateral prominence; the upper part of the prominence is sclerotized and the lower part is membranous (Figs. 36 and 37).

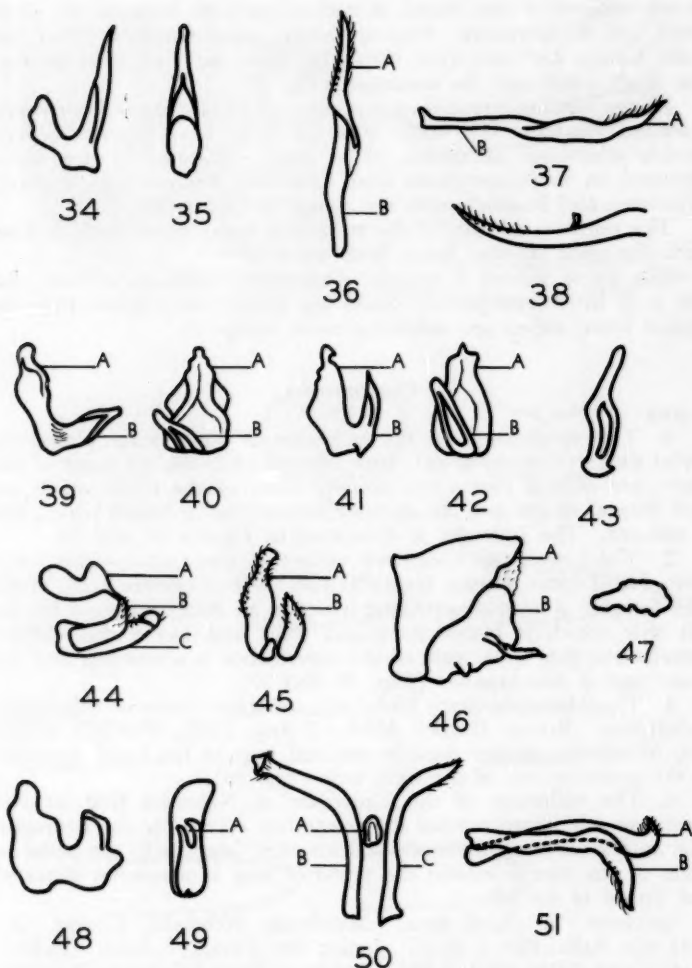
3. The Michigan State University collection contains this insect. Label data: Benton Harbor, Mich.; 2 Aug. 1939. The only distortion found is a slender dorsally directed spur at the basal one-third of the posterior arm of the right style (Fig. 38).

4. The collection of the University of Nebraska contains two specimens which are normal in appearance except for the aedeagus. The anterior arm is broadened and attached laterally to the posterior edges of the lateral valves; the posterior arm is somewhat distorted and tipped to the left.

Specimen "a" label data: Merriman, Nebraska; Cherry Co.; 7/31/32; Salix Fluv.; H. C. Jones; det. *Ceresa bubalus* (Fabr.); H. C. Jones (Figs. 39 and 40). Specimen "b" label data: Baruston, Nebraska; (illegible word) Co.; 7/19/31; Black willow; A. A. Jones; *Ceresa bubalus* (Fabr.); det. H. C. Jones (Figs. 41 and 42).

5. This male is in the collection of the University of Wisconsin. Label data: Amery, Wisconsin; 9-14-17; E. D. Ball, Collector. This is a normal-appearing insect except for the subgenital plate, the aedeagus, the connective and the styles (Figs. 43-45).

The subgenital plate is slightly shorter than usual. The aedeagus appears nearly normal in lateral aspect, but when viewed in posterior



Figs. 34-51.—Male distortions. 34, 35. Aedeagus, specimen No. 1. 34. Left lateral. 35. Anterior. 36, 37. Left style, specimen No. 2. 36. Dorsal; A. Posterior arm; B. Anterior arm. 37. Lateral; A. Posterior arm; B. Anterior arm. 38. Posterior arm of right style, lateral, specimen No. 3. 39, 40. Aedeagus, specimen No. 4a. 39. Left lateral; A. Anterior arm; B. Posterior arm. 40. Posterior; A. Anterior arm; B. Posterior arm. 41, 42. Aedeagus, specimen No. 4b. 41. Left lateral; A. Anterior arm; B. Posterior arm. 42. Posterior; A. Anterior arm; B. Posterior arm. 43-45. Specimen No. 5. 43. Aedeagus, posterior. 44. Connective and styles, left lateral; A. Connective; B. Left style; C. Right style. 45. Styles,

aspect the posterior arm can be seen to be twisted. The connective is shortened and is joined by a thin bit of tissue to the apex of the left style. The right style is short, thick, curved inward at the tip and with only a tiny lobe to indicate the anterior arm. The left style is very short, upturned at the tip and has no indication of an anterior arm.

6. The University of Nebraska collection contains the most distorted male examined. Label data: Brownson, Nebraska; Cheyenne Co.; July 30, '32; rose; H. C. Jones; det. *Ceresa bubalus* (Fabr.); H. C. Jones. The terminalia of this specimen are distorted (Figs. 46-51).

Tergite IX has an irregular posterior margin and has membranous connections with the dorsal parts of the lateral valves. The lateral valves are irregular in shape; the left valve has a long, acute tooth above a short blunt tooth; the right valve lacks the long tooth. The subgenital plate is much reduced, being little more than a tiny, irregular scale.

Both arms of the aedeagus are rather short and thick. The lateral membranes of the posterior arm extend nearly to the top. The functional orifice is dorsal and extends a short distance down the posterior face. At its top, the posterior arm tips to the left. The connective is nearly normal but lacks the notch on the anterior margin. The anterior arms of the styles are short and thick; the posterior arms are strongly divergent at the tips. The posterior arm of the left style curves abruptly ventrally; the posterior arm of the right style has a dorsally recurved tip.

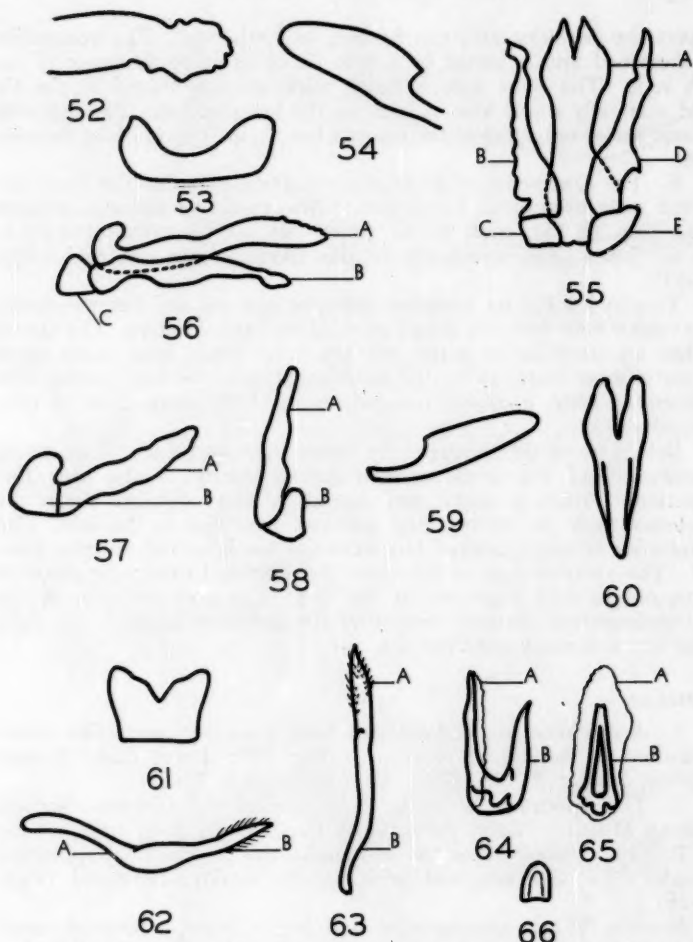
#### FEMALES

1. A specimen in the Michigan State University collection shows distortion of the tip of valvula 2 (Fig. 52). Label data: Benton Harbor, Mich.; 2 Aug. 1939; Ag. College; Lot 1562.

2. This specimen is in the collection of the Chicago Natural History Museum. Label data: Cook Co., Illinois; Col. and pres. by E. B. Chope. Except for the terminalia this is a normal-appearing female. The abdomen and genitalia are weakly sclerotized (Figs. 53-56).

Sternite VII is asymmetrical and has a broad, round-bottomed notch in its posterior margin. Valvulae 1 and valvula 2 are rather twisted-appearing. The left valvula 3 is absent; the right valvula 3 is only slightly distorted; the narrow anterior part is somewhat shorter than usual. The first valvifers are smaller than usual. The second valvifers are absent.

dorsal; A. Right style; B. Left style. 46-51. Specimen No. 6. 46. Tergite IX and left lateral valve, lateral; A. Tergite IX; B. Lateral valve. 47. Subgenital plate, ventral, posterior margin up. 48. Aedeagus left lateral. 49. Aedeagus, posterior; A. Functional orifice. 50. Styles and connective, dorsal; A. Connective; B. Right style; C. Left style. 51. Styles, left lateral; A. Right style; B. Left style.



Figs. 52-60.—Female distortions. 52. Valvula 2 tip, left lateral, specimen No. 1. 53-56. Specimen No. 2. 53. Sternite VII, ventral, posterior margin up. 54. Right valvula 3, lateral. 55. Valvulae 1, valvula 2, first valvifers, dorsal; A. Valvula 2; B. Right valvula 1; C. Right valvifer 1; D. Left valvula 1; E. Left valvifer 1. 56. Valvula 1, valvifer 1, valvula 2, left lateral; A. Valvula 2; B. Valvula 1; C. Valvifer 1. 57-60. Specimen No. 3. 57, 58. Left valvula 1 and left valvifer 1. 57. Lateral; A. Valvula 1; B. Valvifer 1. 58. Ventral; A. Valvula 1; B. Valvifer 1. 59. Right valvula 3, lateral. 60. Valvulae 3, ventral, posterior margin up. Figs. 61-66.—Both male and female parts present, specimen No. 1. 61. Sternite VII, ventral, posterior margin up. 62, 63. Left style. 62. Lateral; A. Anterior arm; B. Posterior arm. 63. Dorsal; A. Posterior arm; B. Anterior arm. 64, 65. Aedeagus. 64. Left lateral; A. Anterior arm; B. Posterior arm. 65. Posterior; A. Anterior arm; B. Posterior arm. 66. Connective, ventral, posterior margin up.

3. The female described here is in the collection of Ontario Agricultural College. Label data: Vineland, Ontario; Chas. A. Small; August 20, 1958. This specimen appears normal except for the genitalia which are distorted and about half normal size (Figs. 57-60).

The condyles near the base of tergite IX are fused in the mid-line. Sternite VII is of the normal shape but is small. Valvulae 1 have a short, thick form and are twisted-appearing. Valvula 2 is represented by remnants. Valvulae 3 are ventrally fused at the mid-line in the basal two-thirds; the narrow basal parts of these valvulae are rather short. The first valvifers are nearly normal. The second valvifers are absent.

#### WITH BOTH MALE AND FEMALE PARTS

1. This specimen is in the collection of Cornell University. Label data: Babylon, L.I., N.Y.; 8-3-1933; F. S. Blanton; *Ceresa bubalis* Fabr.; det. P. W. Oman. This seems to be essentially a distorted male, but it has a sternite VII like a female. There is no other evidence of female parts. Except for the genitalia it appears to be a normal specimen (Figs. 61-66).

The subgenital plate lacks its left tip. But this appears to have been broken or chewed off. The anterior arm of the aedeagus is slender in lateral aspect and somewhat broadened by membranous tissue; the posterior arm is irregular below and with the lateral membranes well below the middle. The ventral lobe of the aedeagus is missing. The connective lacks the anterior notch. The styles are somewhat thickened in the middle and in the posterior arms.

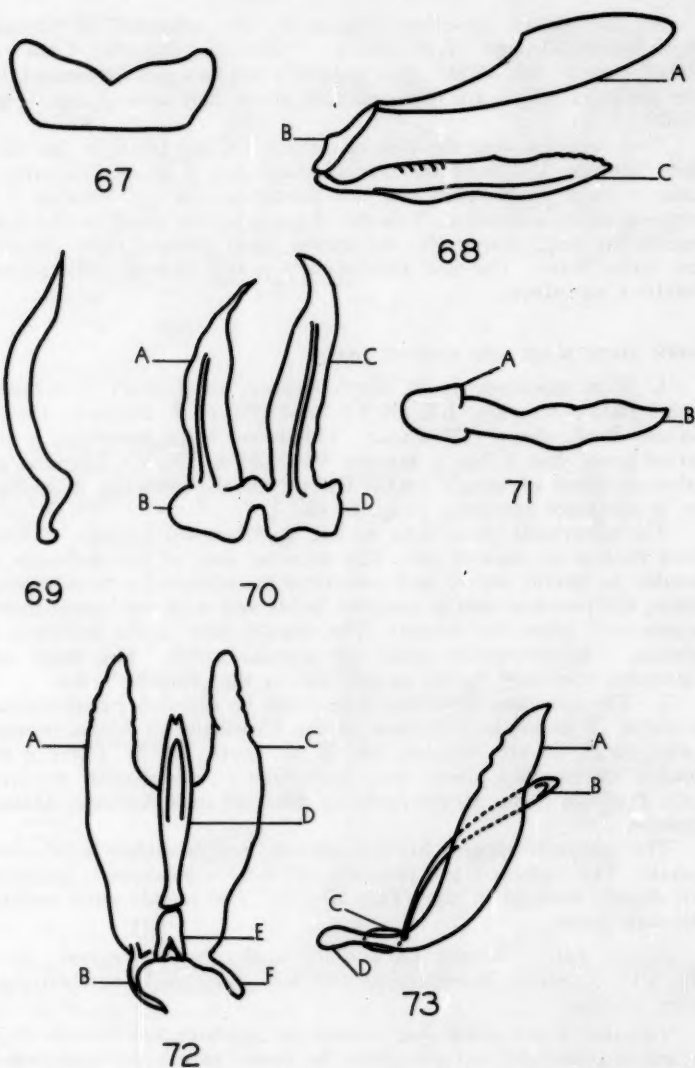
2. The specimen described here could be called a pseudohermaphrodite. It is in the collection of the University of Massachusetts. Label data: *Ceresa bubalus*; det. E. C. Lerch; 1572. There is no locality information given; but, according to information received from Professor Shaw, it was probably collected near Amherst, Massachusetts.

The specimen appears to be a normal, though slightly small-sized female. The abdomen and genitalia are weakly sclerotized; genitalia are slightly reduced in size (Figs. 67-73). The female parts enclose the male parts.

*Female parts.*—Tergite IX and the anal tube are normal. Sternite VII is slightly asymmetrical and has a shallowly notched posterior margin.

Valvulae 1 are somewhat twisted in appearance. Valvula 2 is separated into right and left parts. In lateral aspect the appearance of this valvula is only slightly distorted. However, when seen in ventral aspect, valvulae 2 are crescent-shaped. Valvulae 3 are nearly normal.

The first valvifers are asymmetrical and fused ventrally. The second valvifers are somewhat larger than usual.



Figs. 67-73.—Both male and female parts present, specimen No. 2. 67-71. Female parts. 67. Sternite VII, ventral, posterior margin up. 68. Valvulae 2, 3, valvifer 2, left lateral; A. Valvula 3; B. Valvifer 2; C. Valvula 2. 69. Left valvula 2, ventral. 70. Valvulae 1 and first valvifers, ventral; A. Left valvula 1; B. Left valvifer 1; C. Right valvula 1; D. Right valvifer 1. 71. Left valvula 1

*Male parts.*—The lateral valves and the subgenital plate are missing.

The anterior arm of the aedeagus is absent. The posterior arm is rather slender in lateral aspect; especially toward the base. In anterior aspect this posterior arm can be seen to be slightly broadened at the base, acutely notched at the tip and with the functional orifice incomplete below. The base of the aedeagus articulates with the posterior edge of the connective.

The connective has the notch on the anterior margin deeper than usual and is enclosed in the membranous bases of the posterior arms of the styles.

The anterior arms of the styles are very short; the posterior arms are long and broad and basally fused along their ventral margins for half of their length. The basal parts of the posterior arms are membranous; the distal parts are more heavily sclerotized. Each posterior arm is dorsally coarsely serrate before the tip, presenting an appearance similar to that of valvula 2 of the female.

3. The collection of North Carolina State College contains another pseudohermaphrodite. Label data: Syracuse, N.Y.; 5/22/18; A. J. Basinger, Collector. This specimen otherwise appears to be a normal full-sized female. The genital parts are about two-thirds normal size (Figs. 74-80). The female parts enclose the male parts.

*Female parts.*—Tergite IX and the anal tube are normal. Sternite VII is asymmetrical; its posterior margin is a broad, obtuse notch.

Valvulae 1 are crescent-shaped with a ventral curvature when seen laterally. They are nearly straight in ventral aspect. Valvula 2 is separated into right and left parts. Laterally, they appear twisted and shortened and lack the coarse dorsal serrations before the tip. When viewed in ventral aspect valvulae 2 are crescent-shaped. Valvulae 3 are normal.

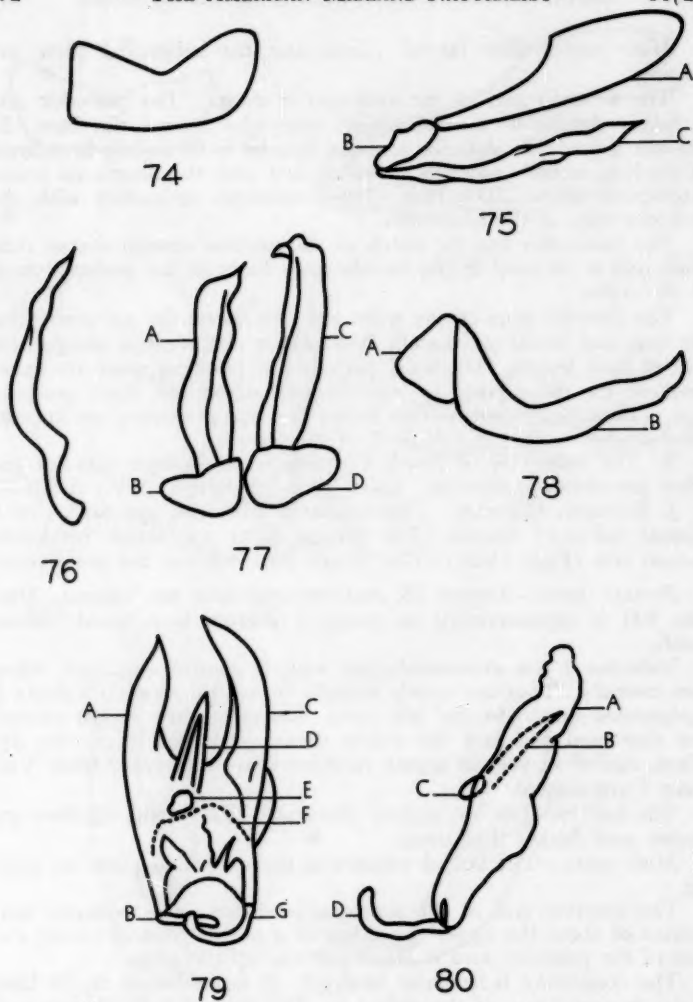
The first valvifers are slightly distorted. The second valvifers are shorter and thicker than usual.

*Male parts.*—The lateral valves and the subgenital plate are lacking.

The anterior arm of the aedeagus is absent. The posterior arm consists of about the upper two-thirds of a normal posterior arm; the base of the posterior arm is about halfway up the styles.

The connective is irregular in shape. It is positioned at the base of the posterior arm of the aedeagus. The base of the aedeagus and the connective are suspended in a hood-like membrane which originates laterally on the styles.

The anterior arms of the styles are convergent and upturned; the and first valvifer, lateral; A. Valvifer 1; B. Valvula 1. 72, 73. Male parts. 72. Anterior; A. Right style, posterior arm; B. Right style, anterior arm; C. Left style, posterior arm; D. Aedeagus; E. Connective; F. Left style, anterior arm. 73. Left lateral A. Left style, posterior arm; B. Aedeagus; C. Connective; D. Left style, anterior arm.



Figs. 74-80.—Both male and female parts present, specimen No. 3. 74-78. Female parts. 74. Sternite VII, ventral, posterior margin up. 75. Valvulae 2, 3, valvifer 2, left lateral; A. Valvula 3; B. Valvifer 2; C. Valvula 2. 76. Left valvula 2, ventral. 77. Valvulae 1 and first valvifers, ventral; A. Left valvula 1; B. Left valvifer 1; C. Right valvula 1; D. Right valvifer 1. 78. Left valvula 1 and first valvifer, lateral; A. Valvifer 1; B. Valvula 1. 79, 80. Male parts. 79. Anterior; A. Right style, posterior arm; B. Right style, anterior arm; C. Left style, posterior arm; D. Aedeagus; E. Connective; F. Membrane; G. Left style, anterior arm. 80. Left lateral; A. Left style, posterior arm; B. Aedeagus; C. Connective; D. Left style, anterior arm.

posterior arms are long and broad and basally fused along their ventral margins for slightly over half of their lengths. The basal, central areas of the styles are weakly sclerotized; the remainder is more strongly sclerotized. Each posterior arm has obscure, coarse dorsal serrations before the tip, presenting an appearance similar to that of the female valvula 2.

#### DISCUSSION

In the male, abdominal tergites IX, X and XI, the lateral valves, the subgenital plate and the connective are rather constant. The teeth of the lateral valves, the styles, the posterior arm and the ventral lobe of the aedeagus have minor variations. The anterior arm of the aedeagus is highly variable.

In the female, abdominal tergites IX, X and XI, abdominal sternite VII, valvifers 1 and 2 and valvulae 1 and 3 are rather constant. Valvula 2 exhibits some variations in the form of dorsal teeth and serrations before the tip.

Only thirteen specimens exhibit any particular distortion, and in four of these the distortion is minor. Reasons for these distortions are unknown. Kornhauser (1919) reported distortion and weak sclerotization of the abdomen and genitalia of the treehopper *Thelia bimaculata* (Fabricius) due to parasitism. In earlier work I found parasites and similar distortions in a few specimens of the treehoppers *Ophiderma salamandra* Fairmaire, *Archasia belfragei* Stal, *Palonica tremulata* (Ball), *Telamona monticola* (Fabricius), *T. tiliae* Ball and *T. spreta* Goding, but no parasites were found in any of the distorted specimens examined during this study.

Except for the anterior arm of the aedeagus and a few variations in valvula 2, the uniformity of the genitalia of the specimens is striking.

Caldwell's (1949) revision of the Ceresini is a step in the right direction. However, it is suggested that the females be considered as well as the males and that a long series of specimens of each species be studied to establish as accurately as possible the amount of variation and uniqueness of genital parts.

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# Physicochemical Properties and Differentiation of Chromatophorotropins and Retinal Pigment Light-Adapting Hormone of the Dwarf Crayfish, *Cambarellus shufeldti*<sup>1</sup>

MILTON FINGERMAN and WILLIAM C. MOBBERLY, JR.  
*Newcomb College, Tulane University, New Orleans, Louisiana*

Recent investigations conducted with the crayfishes *Cambarellus shufeldti* and *Orconectes clypeatus* have been directed toward explaining regulation of pigment migration in the chromatophores and retinal pigment cells (Fingerman, 1957a, b, 1958; Fingerman and Aoto, 1958; Fingerman and Lowe, 1957, 1958; Fingerman, Mobberly, and Sundararaj, 1959). Evidence from these studies supports the hypothesis that the dark red chromatophoral pigment in both species is controlled by dispersing and concentrating substances while the distal retinal pigment is regulated by light-adapting and dark-adapting hormones. Little, however, is known of any relation between chromatophorotropins and retinal pigment activators, e.g., whether these are identical or different substances.

Edman, Fänge, and Östlund (1958), in attempting to isolate red pigment-concentrating hormone from eyestalks of *Pandalus borealis*, reported that the hormone was electronegative at pH 2.5, 4.0, 7.0, and 9.0. They were unable to reverse its charge or to get a positive reaction in the Reindel and Hoppe test for peptides. The hypothesis that neurosecretory products of crustaceans are polypeptides was proposed by Knowles and Carlisle (1956) and is based on physicochemical properties studied by them.

The present investigation was undertaken using *Cambarellus* to determine the electrophoretic behavior of chromatophorotropins at different pH values and to learn whether the retinal pigment light-adapting hormone is identical with or different from the chromatophorotropins in the eyestalk.

## MATERIALS AND METHODS

Specimens of the dwarf crayfish, *Cambarellus shufeldti*, were collected in roadside ditches at Hickory, Louisiana, for use in the experiments described below. The crayfish were kept in aquaria that contained dechlorinated tap water approximately one inch deep.

Extracts of tissues known to contain hormonal substances were assayed on dwarf crayfish from which one eyestalk had been removed at least 12 hours prior to experimental use. Brown, Webb, and Sandeen (1952) and Fingerman (1957a) found that one-eyed individuals were more sensitive to chromatophorotropins than intact specimens.

<sup>1</sup> This investigation was supported by Grant No. B-838 from the National Institutes of Health.

For this reason one-eyed animals were also used in assays for distal retinal pigment light-adapting hormone.

The effect of an extract on body coloration was determined by recording the stages (Hogben and Slome, 1931) of the integumentary dark red chromatophores that lie dorsal to the heart. Stage 1 represents maximal concentration of pigment, stage 5 maximal dispersion, stages 2, 3, and 4 the intermediate conditions. The exoskeleton of *Cambarellus* is sufficiently transparent to allow direct, accurate observation of the underlying chromatophores.

The method of Sandeen and Brown (1952), as modified by Finger-man (1957b) for use with crayfishes, was employed to determine the effect of an extract on the distal retinal pigment of *Cambarellus*. This method entails the following procedure. With the aid of an ocular micrometer and a stereoscopic dissecting microscope the following measurements were made by transmitted light: (1) the width of the translucent distal portion of the eye in a plane parallel to the long axis of the eyestalk and (2) the length of the eye from the corneal surface to the apex of the notch at the proximal portion of the eye. The ratio of length of clear area (measurement 1) to total length (measurement 2) is known as the distal pigment index. Use of this ratio minimizes effects of size differences. The distal pigment index of 10 crayfish can be determined with ease in three minutes.

Potency values were used to facilitate comparison of the effects of different extracts. Values for chromatophorotropins were calculated as described by Sandeen (1950). The stage of the dark red chromatophores of each crayfish receiving chromatophorotropins or control saline (Van Harreveld, 1936) was recorded at the time of injection and 15, 30, 60, 90, and 120 minutes thereafter. The mean chromatophore stage at the start of every experiment was 1.0; the crayfish were in white pans. The six average chromatophore stages for each group of crayfish were summed. Six was then subtracted from the sum because if no dispersion of red pigment had occurred the sum would have been six. Finally, the value of the control group was subtracted from the value obtained from crayfish injected with hormone.

Potency values for extracts containing distal retinal pigment light-adapting hormone were calculated similarly. The mean distal pigment indices recorded 30, 60, 90, and 120 minutes after the extracts and saline had been injected were summed. The sum for the control group was subtracted from the sum of the experimental group and the difference was the potency value. These values have the advantage of taking into account both amplitude and duration of response.

Filter paper electrophoresis was performed in the manner described earlier by Fingerman and Lowe (1957) and Fingerman and Aoto (1958). A model E-800-2 Filter Paper Electrophoresis Apparatus manufactured by the Research Equipment Corporation was used. The voltage was 500 volts and the current 0.1 milliamperes. In the preparation of extracts the excised tissues were triturated in 0.1 ml distilled water. Each extract contained either 40 eyestalks or 20 supraesopha-

geal ganglia with the circumesophageal connectives attached. Extracts of eyestalks were centrifuged to remove the bits of exoskeleton and retinal pigments.

The supernatant was applied in aliquots to a 0.5-inch-wide strip of Whatman No. 1 filter paper. A cool-air blower was used to dry the strip after each application; the entire supernatant was thus contained in a band not more than one-quarter inch wide. The strip of

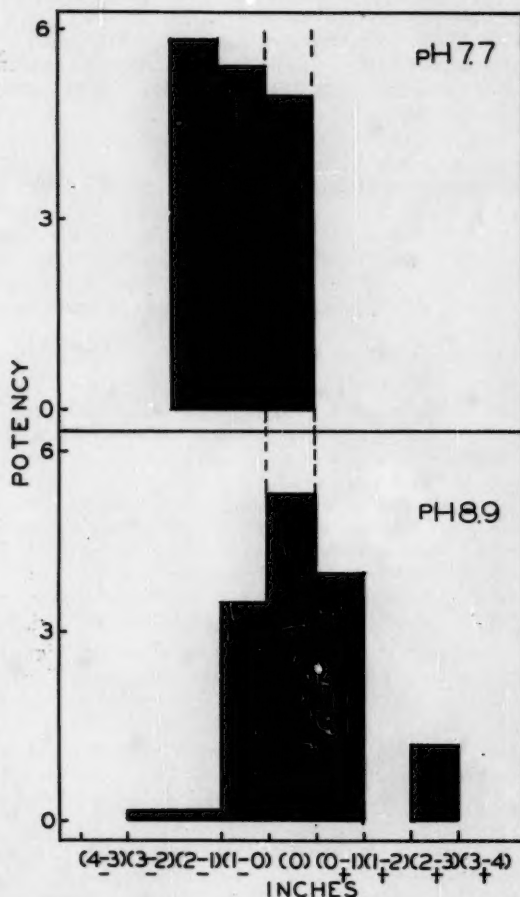


Fig. 1.—Red pigment-dispersing potencies of extracts of eyestalks of *Cambarus* versus position on the filter paper strip after electrophoresis at pH 7.7 and 8.9.

filter paper was then moistened with the appropriate buffer and placed in the electrophoresis migration chamber. The buffers used were 0.1M sodium hydroxide-boric acid for pH values from 7.7 to 9.0 and a mixture of 0.05M citric acid and 0.1M dibasic sodium phosphate of pH 2.3. To minimize the inactivation of chromatophorotropins that occurs when extracts are kept at room temperature (Fingerman and Lowe, 1957) the chamber was kept in a refrigerator maintained at an average temperature of 7°C. After electrophoresis had proceeded for two hours the filter paper strip was removed from the chamber and cut into segments. The number and length of the segments depended upon the experiment. The sections of the strip were placed immediately into 0.3 ml Van Harreveld's solution in covered containers and then kept in the refrigerator for 30 minutes to allow materials to wash from the paper. The fluid was then collected in syringes and 0.02 ml injected into each test animal. Control extracts were prepared by similar elution of segments of buffer-moistened filter paper with 0.3 ml Van Harreveld's solution for 30 minutes.

#### EXPERIMENTS AND RESULTS

##### *Electrophoretic behavior of chromatophorotropins*

The objective of this set of experiments was to determine the direction and distance of migration of chromatophorotropins of *Cambarellus* when filter paper electrophoresis was performed at different pH values. Analyses were performed in the manner described under Materials and Methods.

Extracts of eyestalks were subjected to electrophoresis at pH 7.7 and pH 8.9. The experiment at each pH was performed three times and the results of the corresponding experiments were qualitatively alike. The data obtained at each pH were averaged and the mean potency values were used in the preparation of Figure 1. Inspection of this figure reveals that at pH 7.7 the red pigment-dispersing hormone was electropositive, consequently migration was toward the cathode. At pH 8.9, however, migration occurred toward both poles, but more material remained at the origin than was found in any of the assayed sections of the filter paper strip on either side of the origin. The behavior at pH 8.9 must have been due to reversal of the charge on at least some of the molecules of red pigment-dispersing hormone from the eyestalk. The isoelectric point of this hormone is probably close to pH 8.9.

The next substance investigated was the red pigment-dispersing hormone found in the supraesophageal ganglia and circumesophageal connectives. Fingerman and Aoto (1958) have already shown that the red pigment-dispersing hormone in the supraesophageal ganglia and circumesophageal connectives cannot be the same substance as the red pigment-dispersing hormone found in the eyestalk. One point of evidence was the fact that at pH 7.5 the material in the eyestalk was electropositive as was the case at pH 7.7 (Fig. 1), whereas

the hormone in the supraesophageal ganglia and circumesophageal connectives was electronegative at pH 7.5.

In the present investigation the red pigment-dispersing hormone in the supraesophageal ganglia and circumesophageal connectives was subjected to electrophoresis at pH 2.3 and pH 7.7 (Fig. 2). The experiment at each pH was done three times. At the acid pH the hormone was electropositive, whereas at the higher pH the substance was electronegative. Presumably, its isoelectric point is around pH 5.0.

*Comparison of the electrophoretic behavior of chromatophorotropins and distal retinal pigment light-adapting hormone*

The objective of this set of experiments was to demonstrate that the distal retinal pigment light-adapting hormone is not identical with any of the chromatophorotropins in the eyestalk of *Cambarellus*. The light-adapting and red pigment-dispersing hormones occur in greater quantity than their antagonists in the eyestalks of *Cambarellus* (Fingerman, 1957a; Fingerman, Mobberly, and Sundararaj, 1959). If these hormones do not have the same electrophoretic behavior, then one would be justified in concluding that they are not identical substances.

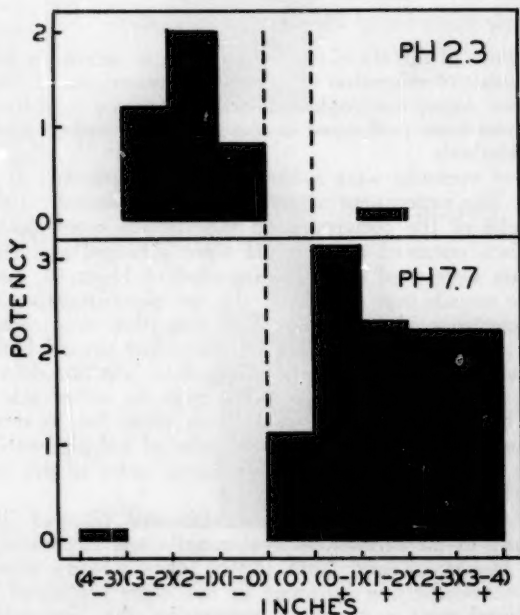


Fig. 2.—Red pigment-dispersing potencies of extracts of supraesophageal ganglia with the circumesophageal connectives attached of *Cambarellus* versus position on the filter paper strip after electrophoresis at pH 2.3 and 7.7.

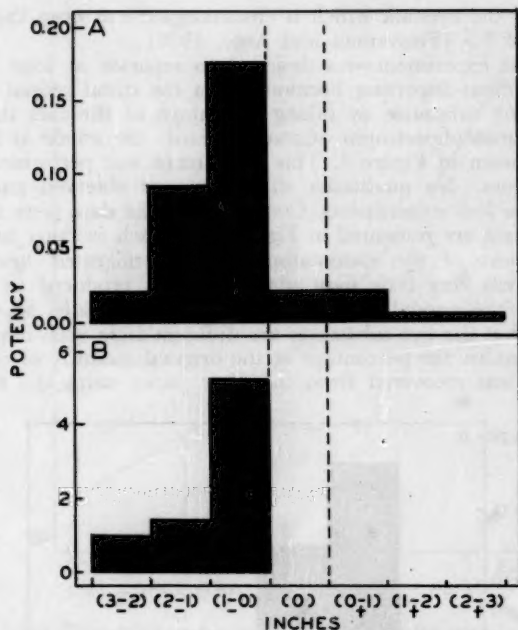


Fig. 3.—Comparison of (A) distal retinal pigment light-adapting potencies and (B) red pigment-dispersing potencies of eyestalk extracts of dwarf crayfish subjected to filter paper electrophoresis at pH 7.8 for two hours.

In the first experiment of this group the pH used was 7.8. One-inch portions on the anodal and cathodal sides of the origin were used in the assay. The extract from each section of the strip was assayed on dwarf crayfish in (1) a white container to determine the red pigment-dispersing potency and (2) a black pan under an illumination of 29 ft.c. to determine the distal retinal pigment light-adapting potency. At this light intensity the distal pigment was in a position approximately midway between the fully light-adapted and dark-adapted positions (Fingerman, Mobberly, and Sundararaj, 1959).

The results of this experiment are shown in Figure 3. The figure shows that the first inch on the cathodal side of the origin contained more light-adapting and red pigment-dispersing hormone than any other section of the strip. The small amounts of light-adapting activity at the origin and on the anodal side were probably not significant. From this figure alone one could not conclude that these substances are different. Since this light-adapting hormone is electropositive at pH 7.8, it could not be identical with the red pigment-concentrating

hormone of the eyestalk which is electronegative at even the slightly lower pH of 7.5 (Fingerman and Aoto, 1958).

The next experiment was designed to separate at least partially the red pigment-dispersing hormone from the distal retinal pigment light-adapting substance by taking advantage of the fact that some of this chromatophorotropin migrates toward the anode at high pH values as shown in Figure 1. This experiment was performed at pH 9.0 four times. No qualitative difference was observed among the results of the four experiments. Consequently, the data were averaged and the means are presented in Figure 4. In each instance an appreciable amount of the chromatophorotropin migrated toward the anode whereas very little light-adaptation was produced by the extracts from the anodal side of the strip. These results support the hypothesis that the two substances are different from each other.

To determine the percentage of the original quantity of each hormone that was recovered from the filter paper strips the following

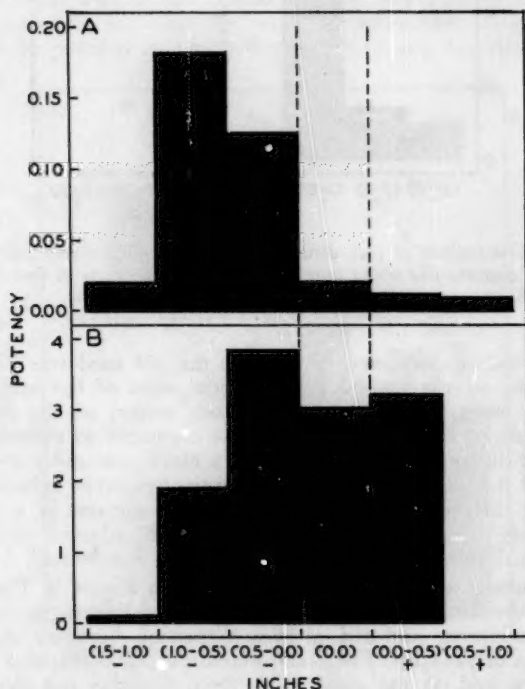


Fig. 4.—Comparison of (A) distal retinal pigment light-adapting potencies and (B) red pigment-dispersing potencies of eyestalk extracts of dwarf crayfish subjected to filter paper electrophoresis at pH 9.0 for two hours.

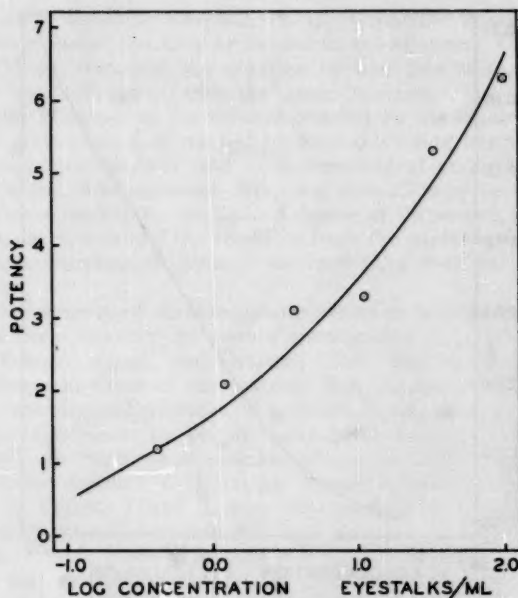


Fig. 5.—Relationship between red pigment-dispersing potency and the logarithm of the concentration of eyestalks of dwarf crayfish.

procedure was employed. Extracts of eyestalks were prepared in six concentrations, 1/243, 1/81, 1/27, 1/9, 1/3 and 1 eyestalk per 0.01 ml Van Harreveld's solution, and injected into dwarf crayfish with maximally concentrated dark red pigment to determine the red pigment-dispersing potency and into *Cambarellus* in black pans under an illumination of 29 ft.c. to obtain the light-adapting potency. Control animals were injected with Van Harreveld's solution. The experiment was performed three times. The concentration in eyestalks/ml that corresponded to the mean potency value obtained with each section of the filter paper strips depicted in Figures 3 and 4 was then read from the corresponding dosage-response curve (Fig. 5 or 6). The potencies of all the sections of each strip were summed and the sum was multiplied by 0.3 because 0.3 ml rather than 1.0 ml of Van Harreveld's solution was used to elute the hormones from each section of the strip. The product was the number of eyestalks equivalent to the amount of hormone recovered from the strip. The values for Figures 3A, 3B, 4A, and 4B were 20.2 eyestalks (50.8% recovery), 12.3 eyestalks (30.3%), 24.8 eyestalks (61.5%), 7.5 eyestalks (18.8%) respectively. The recovery of light-adapting hormone was greater than the recovery of chromatophorotropin (50.8% and 61.5% versus 30.3%

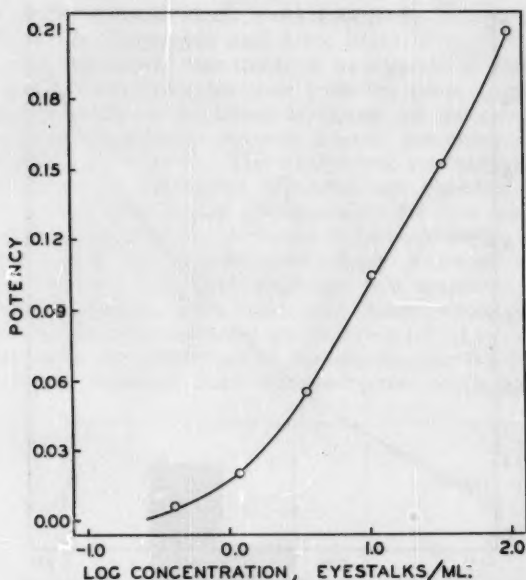


Fig. 6.—Relationship between light-adapting potency and the logarithm of the concentration of eyestalks of dwarf crayfish.

and 18.8%). Two possible explanations of this difference are (1) the chromatophorotropin may be absorbed to filter paper more firmly than the retinal pigment activator and (2) the chromatophorotropin may decay faster than the light-adapting hormone.

#### DISCUSSION

Edman, Fänge, and Östlund (1958) reported that the charge on the red pigment-concentrating hormone of *Pandalus* did not reverse when electrophoresis was performed at pH 2.5, 4.0, 7.0, and 9.0. Red pigment-dispersing hormone in the eyestalk of *Cambarellus* was electropositive at pH 7.7 (Fig. 1) but pH 8.9 appeared to be close to its isoelectric point. Some of the molecules had become electronegative. The results at pH 7.7 (Figs. 1 and 2) were in agreement with those reported earlier at pH 7.5.

The fact that the red pigment-dispersing hormone in the eyestalk is electropositive at pH 7.7, whereas, its functional counterpart in the supraesophageal ganglia and circumesophageal connectives is electronegative at this pH is open to two possible explanations: (1) the two hormones are completely different substances or (2) the same active unit could be attached to either of two proteins. The latter possibility

occurs with thyroxine (Ingbar, 1958). Thyroxine is normally bound to alpha globulin, but may be bound to pre-albumen. Fingerman and Aoto (1958) discussed the question of why one animal would synthesize two substances with the same function. The red pigment-dispersing hormone of the eyestalk reaches its maximum effectiveness more rapidly than does the red pigment-dispersing hormone from the supraesophageal ganglia and circumesophageal connectives (Fingerman, 1957a). The substance from the eyestalk may be used to move the pigment rapidly to the desired degree of dispersion, and once this stage has been attained the hormone from the supraesophageal ganglia and circumesophageal connectives may take over to maintain the condition.

The sensitivity of chromatophorotropins to trypsin and chymotrypsin has been reported by several investigators (e.g., Pérez-González, 1957; Edman, Fänge, and Östlund, 1958) and has been interpreted as evidence in favor of the concept that neurosecretory products in crustaceans are polypeptides. Chromatophorotropins of *Cambarellus* are also inactivated by trypsin (unpublished data). These enzymes, however, also have some esterase activity so that trypsin sensitivity alone is not absolute evidence for a polypeptide. Charge reversal as shown in Figures 1 and 2, however, provides strong evidence for a polypeptide structure rather than an ester one.

Geschwind (1959) discussed the species variation in protein and polypeptide hormones. Two types ( $\alpha$  and  $\beta$ ) of melanophore stimulating hormone (MSH) have been found in the intermediate lobe of pig and ox pituitaries. The  $\alpha$ -form of MSH is a very basic peptide with an isoelectric point between 10.5 and 11.0. Porcine  $\beta$ -MSH is acidic with an isoelectric point of 5.8 and bovine  $\beta$ -MSH has an isoelectric point of 7.0. The substitution of a single amino acid in the molecule accounts for the difference between the isoelectric points of porcine and bovine  $\beta$ -MSH. The occurrence of two forms of MSH in the same pituitary may be analogous to that observed with the red pigment-dispersing hormones in *Cambarellus*. Ultimate determination of the chemical structure of chromatophorotropins in crustaceans may show further similarities between them and  $\alpha$ - and  $\beta$ -MSH.

The authors take pleasure in thanking Dr. L. H. Kleinholz for his helpful suggestions in the preparation of this manuscript. The responsibility for any errors and for the conclusions, however, is entirely our own.

#### SUMMARY AND CONCLUSIONS

1. The red pigment-dispersing hormone in the eyestalk of *Cambarellus* is electropositive at pH 7.7. Its isoelectric point is near pH 8.9.
2. The red pigment-dispersing hormone in the supraesophageal ganglia and circumesophageal connectives is electropositive at pH 2.3, but electronegative at pH 7.7. Its isoelectric point is probably near pH 5.0.
3. The distal retinal pigment light-adapting hormone in the eye-

stalks of *Cambarellus* is not identical with either of the chromatophorotropins found in the eyestalks.

4. The data support the hypothesis that neurosecretory products of crustaceans are polypeptides.

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# Variations Among the Spores of the Microsporidian *Perezia pyraustae* Paillot

JOHN PAUL KRAMER

*Illinois Natural History Survey, Urbana*

## INTRODUCTION

In a previous paper the author (Kramer, 1959) reported the results of a study on the developmental cycle of the microsporidian *Perezia pyraustae* Paillot, an important parasite in the natural control of the European corn borer, *Pyrausta nubilalis* (Hübner) (Kramer, 1959a and 1959b). Among the various stages in the development of *P. pyraustae* and other microsporidians, the spore is of prime importance since it is the infective form of the parasite which is most often transmitted from one host to another. Notable differences are to be found among the spores of *P. pyraustae* recovered from any spore-laden host tissue. The present paper concerns these differences and their probable significance.

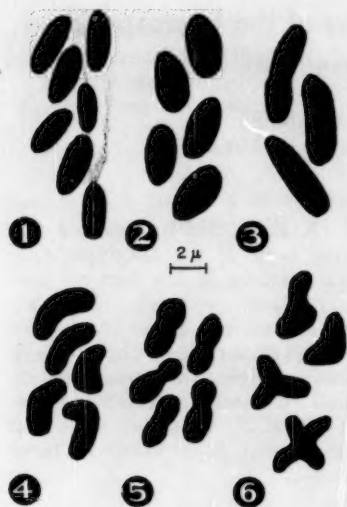
## MATERIALS AND METHODS

At irregular intervals over the past five years the author has examined several thousand larval, pupal, and imaginal *P. pyraustae*-infected *P. nubilalis* collected in Illinois. Among the tens of thousands of *P. pyraustae* spores recovered from feces, haemolymph, fat bodies, silk glands, malpighian tubes, gonads, and ventriculi, several different forms have been observed and are shown in Figures 1-6. While these sketches are based upon spores observed in fixed and stained smears of spore-laden host tissues, similar forms were observed in suspensions of fresh spores in invertebrate saline solution. Smears were briefly air-dried, fixed in a 2 per cent aqueous solution of osmium tetroxide for four to six hours, and stained with Giemsa stain for twelve to thirty-six hours. The nomenclature applied to the various forms of the spore is taken in part from the monumental work of Kudo (1924).

## OBSERVATIONS AND DISCUSSION

In practically all spore-laden host tissues, irrespective of their origin, all types of spores are to be found in varying proportions. A vast majority of the spores are ovocylindrical to ovoidal in form (Figs. 1-2). Not uncommon are the reniform and didymiform types (Figs. 4-5). Rarely one sees the tubular forms (Fig. 3) and the irregular types (Fig. 6). Yet on occasion the author has encountered presumably pure cultures of the ovocylindrical type. Less frequently the author has observed masses of spores which appear to be entirely of the ovoidal type.

Information relating to the significance of these apparent differ-



Figs. 1-6.—Variations in the spores of the microsporidian *Perezia pyraustae* Paillot. 1. Ovocylindrical. 2. Ovoidal. 3. Tubular. 4. Reniform. 5. Didymiform. 6. Irregular.

ences was obtained by measuring several hundred spores selected at random from apparently pure cultures of both the ovocylindrical and ovoidal types. The measuring device was a Leitz OKNOR screw micrometer eyepiece which affords greater accuracy than the standard micrometer scale eyepiece. The length of ovocylindrical spores varied from 2.29 to 3.99  $\mu$  while the length of ovoidal spores ranged from 2.90 to 4.60  $\mu$ . The width of ovocylindrical spores ranged from 1.06 to 1.84  $\mu$  while the width of ovoidal spores varied from 1.13 to 2.35  $\mu$ . Although the length and width of spores varied somewhat independently, an obvious overlap exists between these two spore types. It must be pointed out that the measurements given above are to some extent different from those reported earlier (Kramer, 1959). Doubtless the present measurements are more nearly accurate since they were made with the aforementioned Leitz OKNOR which eliminates to a considerable degree the problem of estimation inherent in the use of the standard micrometer eyepiece which was employed in the earlier study.

The tubular and irregular forms are probably anomalies which result from the absence of cytoplasmic division of sister cells during sporogony. The shape of the reniform and didymiform types probably has been influenced by overcrowding of the parasite population within host cells. The didymiform types in all likelihood result from incomplete separation of sister sporoblasts. It should be noted that the aforementioned reniform and didymiform spores are fairly comparable to the curved and double spores noticed by Hall (1952) in his study of *P. pyraustae* as a parasite in the buckeye caterpillar, *Junonia coenia* Hübner. Of additional interest here is the rather

common occurrence of reniform spores in populations of *P. fumiferanae* Thomson, a parasite of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Thomson, 1959).

The variations observed in the present study pertaining to the ovocylindrical and ovoidal spore types might lead one to suppose that more than one species of microsporidian is present, perhaps even representing two or more genera. This is unlikely since the only recognizable sporonts associated with the spores in question were disporous. This clearly indicates that only the genus *Perezia* is involved. A clue to the real significance of these variations in dimensions lies in the fact that intermediates can be found within any aggregation of microsporidian spores recovered from *P. nubilalis*. Walters (1958) has amply demonstrated a similar type of variation among the spores of a *Nosema* species originally isolated from the cecropia moth, *Hyalophora cecropia* (Linnaeus). These variations in dimensions and the anomalous variations in form (discussed in the preceding paragraph) reflect the sort of differences one might expect in any large population of a single species of Microsporidia or, for that matter, any animal. The obvious conclusion is that until the taxonomic characters used in separating the Microsporidia are more clearly defined, particularly at the species level (see Poisson, 1953), extreme caution should be exercised in the creation of new species based solely upon the dimensions and shape of spores.

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# Litter Size and Latitude in North American Mammals

REXFORD D. LORD, JR.

*Illinois Natural History Survey and Department  
of Conservation, Urbana*

The phenomenon of fluctuations of mammal populations in the higher latitudes of the northern hemisphere is well known. Clearly, population changes of such magnitudes are evidence that large mortality rates are being experienced by these species. Because such large fluctuations in populations seldom occur in the lower latitudes, it seems apparent that species in these latitudes may not often experience the large mortality rates of closely allied species to the north.

The principle of 'inversity' as expressed by Errington (1946) and others, seems to imply that the species of the high latitudes experiencing the high mortality rates will have correspondingly high reproductive rates to help compensate for their losses. Because the breeding season in the north is shorter than that in more southern latitudes, there is less opportunity for increasing reproduction by way of more litters during the season than there is by an increase in the litter size. Therefore, the average litter size of mammals of the same or closely related species should increase with an increase in latitude. Rowan and Keith (1956) for the snowshoe hare and Burns and Burns (1957) for the opossum have shown that such an increase does occur. Moore (in press) has also shown the effect of climate on reproduction in the tree squirrels of the world. To determine if this phenomenon was evident in other mammals a search was made of the literature concerning litter size of mammals of North America.

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## METHODS

The data were grouped according to closely related species because there were not enough data to test the hypothesis statistically for any single species although trends were apparent in several. Data concerning average litter size was preferred to data concerning range in litter size. However, for some groups where data were sparse, the median of the range in litter size was used and when this was done the latitude selected for the species was the median latitude for the range of the species as illustrated in Burt and Grossenheider (1952). Embryo counts alone were used because of the possibility that placental scars would not show resorption.

For those groups in which adequate data were available the slope of the regression was calculated by the method of least squares, and the coefficient of correlation was calculated and tested by the *t* test. For purposes that will become apparent with the progress of this

TABLE I.—Sources of litter size for species

Species	Source	Species	Source	Species	Source
<i>Sylvilagus floridanus</i>		<i>M. californicus</i>	Greenwald (1956)	<i>S. niger</i>	Brown and Yeager (1945)
	Negus (1958)	<i>M. montanus</i>	Hall (1959)		Moore (1957)
	Ecke (1955)	<i>M. townsendi</i>	Hall (1959)		Hoover and Yeager (1953)
	Schwartz (1942)	<i>M. longicaudus</i>	Hall and Kelson (1959)		
	Trippensee (1935)				
	Dalke (1942)	<i>M. mexicanus</i>	Hall and Kelson (1959)	<i>S. alberti</i>	Asdell (1946)
	Gerstell (1937)			<i>S. gerrardi</i>	Asdell (1946)
	Allen (1938)	<i>M. pinetorum</i>	Hall and Kelson (1959)	<i>S. griseus</i>	Asdell (1946)
	Hamilton (1940)			<i>S. apache</i>	Asdell (1946)
	Haugen (1942)	<i>M. quasiater</i>	Hall and Kelson (1959)	<i>Tamiasciurus douglasi</i>	Asdell (1946)
	Beule (1940)			<i>T. fremonti</i>	Asdell (1946)
	Hendrickson (1943)	<i>Peromyscus maniculatus</i>	Coventry (1937)	<i>T. hudsonicus</i>	Asdell (1946)
	Bruna (1951)			<i>Glaucomys volans</i>	Asdell (1946)
<i>S. aquaticus</i>	Lord (1958) (1960)			<i>G. sabrinus</i>	Asdell (1946)
	Hunt (1959)			<i>Eutamias amoenus</i>	Asdell (1946)
	Lowe (1958)			<i>E. cinereicollis</i>	Asdell (1946)
<i>S. auduboni</i>	Sowls (1957)			<i>E. dorsalis</i>	Asdell (1946)
	Hall (1959)	<i>P. leucopus</i>	Davis (1956)	<i>E. minimus</i>	Asdell (1946)
<i>S. idahoensis</i>	Hall (1959)			<i>E. quadrivittatus</i>	Asdell (1946)
<i>S. bachmani</i>	Hall (1959)			<i>E. townsendi</i>	Asdell (1946)
<i>S. nuttalli</i>	Hall (1959)			<i>Tamias striatus</i>	Asdell (1946)
<i>Microtus pennsylvanicus</i>		<i>P. boylii</i>	Coventry (1937)	<i>Lepus arcticus</i>	Hall (1959)
	DeCoursey (1957)	<i>P. californicus</i>	Asdell (1946)	<i>L. americanus</i>	Adams (1959)
	Smith and Foster (1957)	<i>P. eremicus</i>	Jameson (1953)	<i>L. townsendi</i>	Hall (1959)
	Coventry (1937)	<i>P. truei</i>	Asdell (1946)	<i>L. californicus</i>	Asdell (1946)
	Goin (1943)	<i>P. gossypinus</i>	Pournelle (1952)		Lechleiner (1959)
	Harris (1953)	<i>Sciurus carolinensis</i>	Asdell (1946)		
	Asdell (1946)				
<i>M. chrotorrhynchus</i>	Coventry (1937)			<i>L. alleni</i>	Asdell (1946)
<i>M. ochrogaster</i>	De Coursey (1957)			<i>Sorex fumus</i>	Asdell (1946)
	Hall (1959)			<i>S. longirostris</i>	Asdell (1946)

TABLE I.—(continued)

Species	Source	Species	Source	Species	Source
<i>S. palustris</i>	Asdell (1946)	<i>T. bulbivorus</i>	Asdell (1946)		Layne (1958)
<i>S. arcticus</i>	Asdell (1946)	<i>T. douglasii</i>	Asdell (1946)		Layne and McKeon (1956)
<i>S. cinereus</i>	Asdell (1946)				Richards and Hine (1953)
<i>S. dispar</i>	Asdell (1946)				Gier (1947)
<i>S. obscurus</i>	Asdell (1946)	<i>T. talpoides</i>	Asdell (1946)		Sullivan (1956)
<i>S. vagrans</i>	Asdell (1946)	<i>T. townsendi</i>	Asdell (1946)		
<i>Cryptotis parva</i>	Asdell (1946)	<i>Neotoma albigula</i>	Hall (1959)	<i>Alopex berengarius</i>	Asdell (1946)
<i>Microsorex hovi</i>	Asdell (1946)	<i>N. cinerea</i>	Asdell (1946)	<i>A. pribilofensis</i>	Asdell (1946)
<i>Notiosorex craxfordi</i>	Asdell (1946)	<i>N. desertorum</i>	Asdell (1946)	<i>A. lagopus</i>	Asdell (1946)
<i>Blarina brevicauda</i>	Asdell (1946)	<i>N. floridanum</i>	Asdell (1946)	<i>Vulpes velox</i>	Asdell (1946)
<i>B. taylori</i>	Asdell (1946)	<i>N. lepida</i>	Asdell (1946)	<i>Martes americana</i>	Asdell (1946)
<i>Spermophilus</i>		<i>N. magister</i>	Asdell (1946)	<i>M. pennanti</i>	Asdell (1946)
( <i>Citellus</i> ) <i>parryi</i>	Asdell (1946)	<i>N. mexicana</i>	Asdell (1946)	<i>Mustela vison</i>	Asdell (1946)
<i>S. tridecemlineatus</i>	Asdell (1946)	<i>N. micropus</i>	Asdell (1946)	<i>M. frenata</i>	Asdell (1946)
<i>S. townsendi</i>	Asdell (1946)	<i>Vulpes vulpes</i>	Scott, T. G.	<i>M. rixosa</i>	Asdell (1946)
<i>S. tereticaudus</i>	Asdell (1946)	=( <i>fulva</i> )	(unpublished)	<i>M. cicognani</i>	Asdell (1946)
<i>S. franklini</i>	Asdell (1946)		Sheldon (1949)	<i>Taxidea taxus</i>	Asdell (1946)
<i>S. harrisi</i>	Asdell (1946)		Schofield (1948)	<i>Gulo luscus</i>	Asdell (1946)
<i>S. beldingi</i>	Asdell (1946)		Switzenburgh (1950)	<i>Lutra canadensis</i>	Asdell (1946)
<i>S. mohavensis</i>	Asdell (1946)		Layne and McKeon (1956)	<i>Mephitis mephitis</i>	Asdell (1946)
<i>S. idahoensis</i>	Asdell (1946)		Hoffman and Kirkpatrick (1954)	<i>M. macroura</i>	Asdell (1946)
<i>S. lateralis</i>	Asdell (1946)		Richards and Hine (1953)	<i>Spilogale putorius</i>	Asdell (1946)
<i>S. leucurus</i>	Asdell (1946)		Gier (1947)	<i>Felis concolor</i>	Asdell (1946)
<i>S. richardsonii</i>	Asdell (1946)		Sheldon (1949)	<i>F. pardalis</i>	Asdell (1946)
<i>S. spilosoma</i>	Asdell (1946)			<i>F. onca</i>	Asdell (1946)
<i>S. variegatus</i>	Asdell (1946)			<i>Lynx rufus</i>	Asdell (1946)
<i>S. washingtoni</i>	Asdell (1946)			<i>L. canadensis</i>	Asdell (1946)
<i>Geomys brevipes</i>	Wood (1949)			<i>Rattus norvegicus</i>	Davis (1953)
<i>Thomomys bottae</i>	Asdell (1946)			<i>R. rattus</i>	Davis (1953)
		<i>Urocyon cinereoargenteus</i>	Wood (1958)		

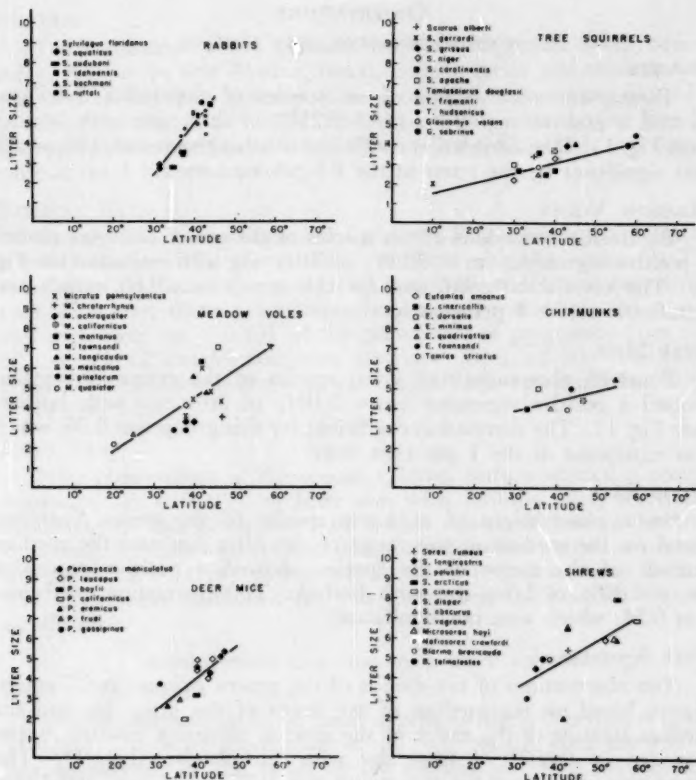


Fig. 1.—Mammals which showed a statistically significant positive correlation of litter size with latitude.

paper, the groups were arranged into three categories: prey species that do not hibernate, prey species that do hibernate, and predatory species. Table I lists the reference according to species from which the litter size data were obtained.

To test the consistency of the findings obtained from such a wide variety of sources which were probably collected by a variety of methods, the data from eight years of the North American Census of Small Mammals (Calhoun and Arata, 1950-1957) were analyzed for the relation of litter size to latitude in closely allied species. The data obtained from this source were all obtained from a standardized trap census.

## OBSERVATIONS

## NON-HIBERNATING PREY SPECIES

## RABBITS

Twenty-one observations of six species of the genus *Sylvilagus* plotted a positive regression ( $m = 0.251$ ) of litter size with latitude (see Fig. 1). The correlation coefficient for this group was 0.83, which was significant by the  $t$  test at the 0.1 per cent level.

## MEADOW VOLES

Eighteen observations of ten species of the genus *Microtus* plotted a positive regression ( $m = 0.133$ ) of litter size with latitude (see Fig. 1). The correlation coefficient for this group was 0.69, which was significant at the 1 per cent level.

## DEER MICE

Fourteen observations of seven species of the genus *Peromyscus* plotted a positive regression ( $m = 0.160$ ) of litter size with latitude (see Fig. 1). The correlation coefficient for this group was 0.66, which was significant at the 1 per cent level.

## WOOD RATS

Seven observations of as many species of the genus *Neotoma*, based on the median of the range of the litter size and the median latitude of the range of the species, showed a positive regression ( $m = 0.086$ ) of litter size with latitude. The correlation coefficient was 0.54, which was not significant.

## TREE SQUIRRELS

Ten observations of ten species of the genera *Sciurus* and *Tamiasciurus*, based on the median of the range of the litter size and the median latitude of the range of the species, plotted a positive regression ( $m = 0.052$ ) of litter size with latitude (see Fig. 1). The correlation coefficient for this group was 0.80, which was significant at the 1 per cent level.

## CHIPMUNKS

Seven observations of seven species of the genera *Eutamias* and *Tamias*, based on the median of the range of the litter size and the median latitude of the range of the species, plotted a positive regression ( $m = 0.049$ ) of litter size with latitude (see Fig. 1). The correlation coefficient for this group was 0.50, which was not significant, probably because of the small sample.

## HARES

Five observations of five species of the genus *Lepus*, based on the median of the range of the litter size and the median latitude of the range of the species, plotted a positive regression ( $m = 0.091$ ) of litter size with latitude. The correlation coefficient was 0.66, but was not significant due to the small sample.

## SHREWS

Twelve observations of as many species of the genera *Sorex*, *Microsorex*, *Notiosorex* and *Blarina*, based on both mean and median litter size and the median latitude of the range of the species, plotted a positive regression ( $m = 0.120$ ) of litter size with latitude (see Fig. 1). The correlation coefficient for this group was 0.65, which was significant at the 1 per cent level.

## NORWAY RATS

Twenty-five observations of the species (*Rattus norvegicus*) plotted a positive regression ( $m = 0.027$ ) of litter size with latitude. The correlation coefficient for this group was 0.26, which was not significant. However, thirty-two observations of this species plotted a positive regression ( $m = 0.45$ ) of the prevalence of pregnancy (per cent of a sample of females that were pregnant) with latitude. The correlation coefficient for this group was 0.35, which was significant at the 5 per cent level.

## ROOF RATS

Nine observations of the species (*Rattus rattus*) plotted a positive regression ( $m = 0.049$ ) of litter size with latitude. The correlation coefficient for this group was 0.69, which was significant at the 5 per cent level. In this same species, fifteen observations plotted a negative regression ( $m = -0.18$ ) of the prevalence of pregnancy with latitude. The correlation coefficient for this group was 0.20, which was not significant.

## HIBERNATING AND FOSSORIAL PREY SPECIES

## GROUND SQUIRRELS

Fifteen observations of as many species of the genus *Spermophilus* (*Citellus*), based on the median of the range of the litter size and the median latitude of the range of the species, plotted a regression of nearly zero ( $m = 0.009$ ) with latitude (see Fig. 2). The correlation coefficient was 0.06, which was not significant.

## POCKET GOPHERS

Six observations of six species of the genera *Geomys* and *Thomomys*, based on both mean litter size and the median of the range of the litter size and the median latitude of the range of the species, plotted a nearly zero ( $m = 0.018$ ) regression with latitude (see Fig. 2). The correlation coefficient was 0.14, which was not significant.

## PREDATORS

## RED FOX

Fourteen observations of this species (*Vulpes vulpes = fulva*), based on mean litter size as determined by 14 studies of the species at different locations in the United States, plotted a negative regression ( $m = -0.289$ ) of litter size with latitude (see Fig. 2). The correlation coefficient for this species was 0.41, which was not significant.

## GRAY FOX

Six observations of this species (*Urocyon cinereoargenteus*), based on mean litter size, plotted a slightly negative regression ( $m = -0.029$ ) of litter size with latitude (see Fig. 2). The correlation coefficient for this species was 0.36, which was not significant.

## FOXES

Six observations of six species of the genera *Alopex*, *Vulpes* and *Urocyon*, based on the median of the range of the litter size and the median latitude of the range of the species, plotted a positive regression ( $m = 0.078$ ) of litter size with latitude (see Fig. 2). The correlation coefficient for this group was 0.60, which was not significant.

## MUSTELIDS

Twelve observations of as many species of the genera *Martes*,

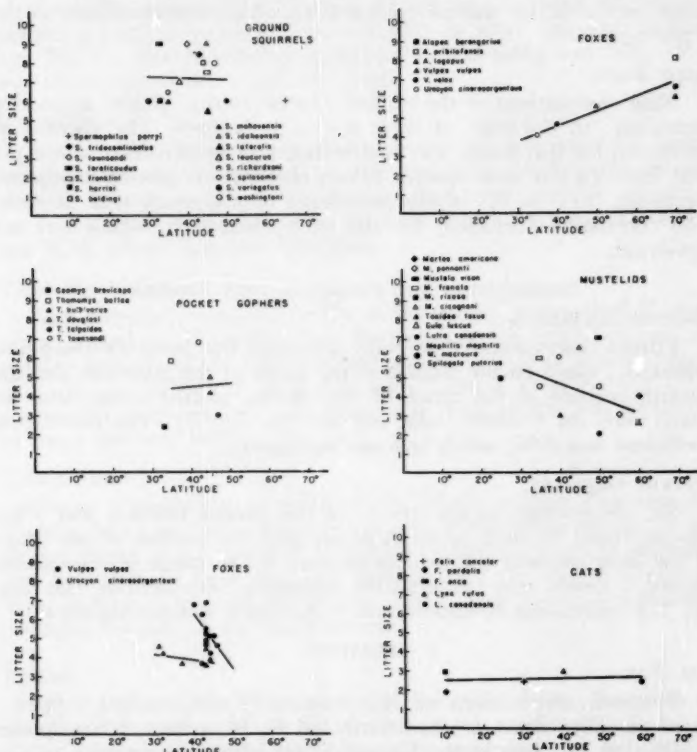


Fig. 2.—Mammals which showed no significant correlation of litter size with latitude.

*Mustela*, *Taxidea*, *Gulo*, *Lutra*, *Mephitis* and *Spilogale* based on the median of the range of the litter size and the median latitude of the range of the species, plotted a negative regression ( $m = -0.061$ ) of litter size with latitude (see Fig. 2). The correlation coefficient for this group was 0.32, which was not significant.

#### CATS

Five observations for as many species of the genera *Felis* and *Lynx*, based on the median of the range of the litter size and the median latitude of the range of the species (in North America), showed no regression ( $m = 0.003$ ) of litter size with latitude (see Fig. 2). The correlation coefficient for this group was 0.11, which was not significant.

#### NORTH AMERICAN CENSUS OF SMALL MAMMALS

From the data compiled by Calhoun and Arata (1950-1957) only two genera, *Peromyscus* and *Microtus*, contained sufficient material for statistical analysis of the relation of embryo counts to latitude. In the genus *Peromyscus* twenty-four observations plotted a positive regression ( $m = 0.089$ ) of litter size with latitude. The correlation coefficient for this group was 0.59, which was significant at the 1 per cent level. In the genus *Microtus* seventeen observations plotted a positive regression ( $m = 0.075$ ) of litter size with latitude. The correlation coefficient for this group was 0.53, which was significant at the 5 per cent level.

#### DISCUSSION

It is apparent from the observations that only a certain portion of the groups examined fulfilled the expectations of the thesis of this paper. Only the non-hibernating prey species seem to have increasingly larger litters which approach toward the polar region. Both the hibernating and fossorial prey species and the predators, with the possible exception of the foxes, appear to be unaffected by latitude with reference to litter size.

The role of hibernation in this phenomenon appears to be supported by the tree squirrels, chipmunks and wood rats, all of which are partial hibernators; that is, they are known to remain in their holes or nests during periods of extremely adverse weather during the winter. These same species showed a lower gradient of increase of litter size with increase in latitude.

The plain implication is, that whatever the factor is that is working on these animals, be it compensation for high mortality or something else, it is operating in the winter upon those prey species which are exposed. And just as plainly it appears not to affect the predators, except possibly the foxes.

The foxes present a puzzling situation. There appears to be a positive relation between litter size and latitude when the four species of fox found in North America are compared. But there happens to be much literature available on embryo counts of foxes made by many

workers in different parts of the United States. These data actually show a reverse or negative relationship between litter size and latitude in the red fox. While this relationship was not statistically significant, a study by Schofield (1957) showed a significant difference in litter size of red foxes between the Upper Peninsula, the northern Lower Peninsula, and the southern Lower Peninsula of Michigan. In this case litter size became successively larger from north to south. Layne (1956) found different litter sizes in three regions of New York state, but here the region with the largest litters was located between the regions with successively smaller litters. Both in New York and in Michigan the litter size of the red foxes appears to be inversely related to the density of breeding populations of foxes which in Michigan was dependent on human predation.

In the case of mustelids, the necessity to combine so many different genera to obtain a sufficient number of observations for statistical treatment may have resulted in the apparent lack of correlation between litter size and latitude in this group. However, no closely related group within this family, such as the skunks, showed any tendency to exhibit a correlation.

Lack (1946) described a similar phenomenon in birds, that is, larger clutch size in high latitudes. In birds the explanation appears to be related to their ability to secure more food for their young due to the greater day length. In mammals it is difficult to believe that the increased day length would have any positive relation to the increased litter size, because many of the groups are inherently nocturnal and are actually forced to seek food in the light due to the long arctic summer day. The apparent lack of response of the hibernators and the predators also would be inexplicable by this theory. More explicable is the theory that the increased litter size is directly related to the mortality sustained by the species. This is a rather universal phenomenon and its application here is only slightly different from its more traditional applications. One possible explanation of the method through which it operates is provided by the work by Christian and Lemunyan (1957) which showed smaller litters in the more dense breeding populations. Thus the hibernators, which escape the severe mortality of the winter, emerge in the spring with relatively greater population densities than the non-hibernating species. Therefore, the hibernators should have relatively smaller average litters. Farther south the winters are milder and presumably the winter mortality among non-hibernators is lower, resulting in more dense spring breeding populations and thus, smaller average litters.

However, the severity of the winter weather in the higher latitudes has probably been a force for selecting animals with large litters.

The test of the consistency of the findings from the varied sources by analysis of the data from the North American Census of Small Mammals again found a positive correlation between litter size and latitude in both *Peromyscus* and *Microtus*.

The data compiled by Davis (1953) for both Norway and Roof

rats contained information concerning prevalence of pregnancy in addition to litter size data. Analysis of this information showed a significant positive correlation between prevalence of pregnancy and latitude in the Norway rat but not in the Roof rat. Both species showed positive correlation of litter size with latitude although the coefficient of correlation was significant for the Roof rat only. Thus, it is apparent that those forces which are correlated with latitude that cause the increase in litter size with increasing latitude might also cause an increase in the prevalence of pregnancy.

Workers interested in investigating this phenomenon more thoroughly should make periodic collections throughout the breeding season as frequently as the length of the gestation period of the species being investigated. Data should be collected concerning both prevalence of pregnancy and average litter size. Analysis of data collected in this manner can give the mean annual production of young per female.

#### SUMMARY

Analysis of the data concerning litter size in relation to latitude in North American mammals has shown statistically significant positive correlation for six groups of closely related non-hibernating prey species. Two groups of hibernating and fossorial prey species and the predators, with the possible exception of the foxes, showed no relation between litter size and latitude. Possibly the relation reported by other workers between mortality and reproduction is, at least in part, dependent on an inverse relationship between density of breeding adults and litter size. Also the severity of the winter weather in the higher latitudes has probably been a selective force for larger litters.

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## Notes and Discussion

### A Northernmost Record of *Plecotus rafinesquii* Lesson (Mammalia, Chiroptera).

The previous northernmost record of a species of *Plecotus* for the eastern United States was based upon a specimen collected five miles southwest of Greencastle (Putnam County), Indiana (A. W. Butler, 1895, Proc. Indiana Acad. Sci. for 1894:86). Butler's specimen is presumably lost and there has been some doubt among mammalogists as to which species this record should be referred. Hall and Kelson (The Mammals of North America, p. 200, 1959) referred the record to *P. townsendii virginianus* (Handley). On the other hand, Handley (Proc. U. S. Nat. Mus., 110:165, 1959) believed it to be referable to *P. rafinesquii rafinesquii* Lesson.

On December 13, 1959, I collected a male of Rafinesque's big-eared bat, *P. rafinesquii*, from a concrete conduit along Indiana Highway 43, 1.3 miles north of West Lafayette (Tippecanoe County). The conduit is in a wooded area and empties into the Wabash River some 700 feet away. The bat was hanging from the ceiling of a side shaft 137 feet from the nearest outside opening.

Over the past three winters, the conduit had been checked 42 times in studying hibernation in a small group of the big brown bat, *Eptesicus fuscus* (Palisot de Beauvois). This is the first bat of another species to be found. The most recent trip, prior to December 13, was on December 6, at which time only two individuals of *E. fuscus* were present.

This is the sixth time, including Butler's record, that this bat has been collected in Indiana. It extends the known range by 59 miles from the previous northernmost record of a species of *Plecotus* in the eastern United States and by 120 miles from the previous northernmost record of *P. r. rafinesquii* based upon an extant specimen. This collection falls into a pattern noted by Handley (*op. cit.*: 157); that is, that all northern specimens have been taken or recorded in caves or cave substitutes during the cooler months of the year.

The specimen (No. NW 248 in my collection) had the following measurements: total length, 104 mm; tail, 48 mm; hind foot, 10 mm; ear, 35 mm; tragus, 13 mm; forearm, 45 mm; wingspread, 305 mm; and testes 2 x 4 mm. It weighed 10.5 grams with considerable subcutaneous fat present in the inguinal and lower back region. The stomach contained several specimens of the nematode, *Capillaria palmatus* Chandler (U. S. Nat. Mus. Helm. Coll. No. 56620), identified through Doctor Allen McIntosh of the Animal Disease and Parasite Research Branch, U. S. Department of Agriculture.—NIXON WILSON, Department of Entomology, Purdue University, Lafayette, Indiana.

### A Congenital Diaphragmatic Hernia in the Raccoon

A captive group of raccoons (*Procyon lotor*) has been maintained for research purposes in Urbana, Illinois, since the fall of 1956. On April 15, 1959, a female, bred in captivity, gave birth to a litter of three males which were removed from their mother on June 9, 1959, and reared together in another cage.

On July 7, 1959, one of the males was castrated in order to study the

effects of castration on the maturation rate of the skeleton. This operation caused no decline in growth of the animal or other apparent ill effects.

This male was found dead in the cage on September 30, 1959. He was in good physical condition and weighed 7.1 lbs., while his litter mates weighed 7.5 and 6.4 lbs., respectively. At autopsy the entire stomach and approximately four inches of the duodenum were found in the left thoracic cavity. The stomach and duodenum appeared to be normal; there were no signs of strangulation of the duodenum, no adhesions, and no indication of rupture or inflammation around the small hole in the diaphragm through which the stomach and duodenum had entered into the thoracic cavity. The raccoon showed no other obvious signs of illness and otherwise appeared to be in good health. It appears that he died of suffocation when the stomach entered the thoracic cavity and put pressure on his lungs. Because of the points just mentioned, plus the fact that body weight was normal, the hernial opening is believed to be congenital; but the stomach and duodenum probably remained in their normal positions until a short time prior to death. Lung, stomach and intestinal tissue of the raccoon were not congested, indicating that he probably died within minutes after the stomach entered the thoracic cavity.

According to Secord, most cases of acquired diaphragmatic hernia in the dog occur as a result of injury (*Canine Surgery*, Amer. Vet. Publs., Inc., 4th ed. 1957:404). However, the cages in which the raccoons were kept were protected by a high wire fence with a locked gate so it is unlikely that this male was injured by humans or animals outside the cage.

Because he was reared with his litter mates there is little chance that there was any injury because of the normal playing and "fighting" among the young raccoons in their cage. Although Secord reports that being run over by an automobile is the most common direct cause of diaphragmatic hernia in the dog, he does indicate that some cases in young puppies and kittens are congenital. Most of such animals are stunted with the stomach permanently lodged in the thoracic cavity. This author also states that in a left-sided hernia involving the stomach, death may be caused by asphyxiation because of the pressure on the lungs from the bloated stomach.

R. M. Thomas, D.V.M., Instructor of Veterinary Pathology and Hygiene, University of Illinois, College of Veterinary Medicine, also examined this animal and confirmed this diagnosis.—GLEN C. SANDERSON, Illinois Natural History Survey, Urbana.

### *Eleocharis elliptica* and *E. compressa*: Further Notes and Corrections

When the authors in their recent study of *E. compressa* and *E. elliptica* (Am. Midl. Nat. 63:143-148. 1960) combined these two taxa into the same species, we erroneously stated that *E. compressa* had priority over *E. elliptica*. However, *E. elliptica* Kunth (1837) clearly antedates *E. elliptica* Sullivant (1842). This lapse has kindly been called to our attention by Dr. E. G. Voss.

As a result of this, typical material of *E. elliptica* should be known as *E. elliptica* Kunth var. *elliptica*, while the specimens with compressed culms should be made a further variety of *E. elliptica*. The question then arose as to the varietal epithet that should be used. It happens that there is already a varietal epithet in *E. compressa*: var. *atrata* Svenson. It then became necessary to examine the type collection of var. *atrata*.

Svenson named var. *atrata* from a specimen collected by Pease (No. 12991) from Presque Isle, Pennsylvania. The authors wish to thank Dr. Clarence Kobuski of the Gray Herbarium for kindly loaning the specimen.

After a careful study of the type (there are three specimens on the sheet), it was clear that here we were dealing with a plant much more closely related to *E. elliptica* than to *E. compressa*. Two of the three specimens had 6 vascular bundles per culm while the third specimen possessed 8. The scales of each plant were deep purple-brown (not blackish) while the basal sheaths were reddish. No differences could be observed in achene characters.

Although Fernald (Gray's Manual of Botany, 8th ed. 1950. Pg. 258) gives the range for var. *atrata* as "shores of Great Lakes," etc., a recheck of Illinois material shows plants with scale color identical to the type specimen as occurring throughout Illinois. The color of the basal sheaths varies with these dark-scaled specimens.

In re-evaluating the situation, the taxon *E. compressa* var. *atrata* seems nothing more than a dark-scaled form of typical *E. elliptica*. *Eleocharis compressa* may then be known as var. *compressa* of *E. elliptica*.

The citation for these taxa should be corrected to:

*ELEOCHARIS ELLIPTICA* Kunth var. *ELLIPTICA*

*Eleocharis elliptica* Kunth, Enum. 2:146. 1837.

*Eleocharis capitata* var. *borealis* Svenson in Rhodora 34:202. 1932.

*Eleocharis tenuis* var. *borealis* (Svenson) Gleason in Phytologia 4:22. 1952.

*Eleocharis compressa* var. *borealis* (Svenson) Drapalik & Mohlenbrock, Am. Midl. Nat. 63:147. 1960, nomen illeg.

*ELEOCHARIS ELLIPTICA* Kunth var. *ELLIPTICA* f. *ATRATA* (Svenson) Drapalik & Mohlenbrock, comb. nov.

*Eleocharis compressa* var. *atrata* Svenson in Rhodora 34:218. 1932.

*ELEOCHARIS ELLIPTICA* Kunth var. *COMPRESSA* Drapalik & Mohlenbrock, stat. nov.

*Eleocharis compressa* Sulliv. in Am. Jour. Sci. 42:50. 1842.

—DONALD J. DRAPALIK and ROBERT H. MOHLENBROCK, Southern Illinois University, Carbondale.

### American Institute of Biological Sciences Translation Program

The American Institute of Biological Sciences is currently translating and publishing seven Russian research journals in biology. These journals are translated with support from the National Science Foundation, which is eager that such information be more widely distributed to biologists throughout the world. It is hoped that this material will aid biologists in research, prevent duplication of work, give some idea of the work being done by Soviet scientists in the field of biology, and also bring about a better international understanding among scientists.

Because of the support of the National Science Foundation, the AIBS can offer these translations at a fraction of their publication cost, with even further price reduction to AIBS members and to academic and non-profit libraries. This reduction, the AIBS feels, places the translation within the reach of all biologists.

The journals currently being translated are: *Doklady: Biological Sciences Section*; *Doklady: Botanical Sciences Section*; *Doklady: Biochemistry Section*; *Plant Physiology*; *Microbiology*; *Soviet Soil Science*; and *Entomological Review*.

In addition to its program of Russian Biological Journal translations, the AIBS has instituted a separate program of translation and publication of selected Russian Monographs in biology.

It was felt that the program of Journal translations was not sufficient

to cover all of the significant work being done in all fields of biology by Russian scientists. With the aid of competent authorities, the AIBS has translated and published six Russian monographs and one monograph is in the process of being published. In addition, several prominent monographs in various biological areas are being considered by the AIBS and the National Science Foundation for translation and publication. The monographs that have been published are: *Origins of Angiospermous Plants* by A. L. Takhtajan; *Problems in the Classification of Antagonists of Actinomycetes* by G. F. Gauze; *Marine Biology*, Trudi Institute of Oceanology, Vol. XX, edited by B. N. Nikitin; *Arachnoidea* by A. A. Zakhvatkin; and *Arachnida* by B. I. Pomcrantzев. The manuscript for *Plants and X rays* by L. P. Breslavets is in the final stages of preparation and should be published early in 1960.

Additional information pertaining to this program may be obtained by writing to the American Institute of Biological Sciences, 2000 P Street, N. W., Washington 6, D. C., U. S. A.

## Book Reviews

THE RUSTY LIZARD. A POPULATION STUDY. W. Frank Blair. University of Texas Press, Austin. 1960. xiv+183; 31 Figs. \$4.50.

This book on *Sceloporus olivaceus* is one of the most significant studies of a natural population of vertebrates, easily equalling in scope and importance the classic reptile studies of Fitch in North America and of St. Girons and Volsøe in Europe. Dr. Blair's study is of particular note ecologically because it covers a five-year period during one of the severest droughts in history in central Texas. It has often been stated that consideration of extreme conditions is most important in studies of adaptation and evolution; in this investigation data are presented on the mechanisms by which this population was able to maintain its numbers during a period of climatic extremes.

Basically, the book deals with the populations dynamics of this arboreal lizard on a ten-acre tract near Austin, Texas. Approximately 3000 lizards were trapped, noosed, or collected by hand and marked in various ways for individual identification in order to follow their dispersion, home range establishment, growth, reproduction and mortality. The environment of the lizards is described in detail including such aspects as vegetation and vegetational changes, actual or potential predators, possible competitors and food supply.

Most of the significant data are included in two chapters dealing with adaptation by the individual and adaptation by the population. In the first of these mating, growth rate, loss and regeneration of the tail, ontogenetic pattern changes, body temperature, diel cycle and escape behavior are the fundamental topics considered. No new generalizations or phenomena are reported, but excellent information on growth from numerous recoveries of marked animals over long periods is made available. My only criticism of this section is of what appears to be a lack of balance between the topics. For example, temperatures were obtained apparently of only a dozen lizards during the study and less than a page is devoted to this aspect of lizard ecology; in contrast, 11½ pages and a number of tables are devoted to tail growth and regeneration—more pages than are devoted to growth of the individual.

The chapter dealing with adaptation by the population is concerned primarily with how the breeding population of adults was maintained during the adverse period covered by the study. Most mortality was due to nest failure and loss of juveniles for several reasons. Very little effect was noted from food shortage which seemed to play a minor role in the ecology of these lizards. The population of breeding adults remained fairly constant due in part to an extremely high (for reptiles) reproductive potential and in part to an apparently greater percentage survival of young lizards during seasons when population density and reproduction were low than when density and egg production were high. Too, immigration plays some part in stabilizing the density of lizards.

The last part of the book concerning organization of the population contains material on sex ratios, movement and dispersal, home ranges and social interactions. It appears that the sex ratio, unbalanced in favor of females in the older age classes, is an adaptation for obtaining maximum reproduction in a promiscuous mating system. One male can fertilize several females and a disparate sex ratio removes older males from intraspecific com-

petition with the reproductive element of the population. Home ranges, once established, remain fairly stable for years and are organized around suitable trees, the availability of which appears to set the upper limit for the adult population.

Only one omission of data that might have been obtained was evident to this reviewer. Number of layings per season are reported, as is mating behavior and copulation, but there is no information of whether or not each laying is preceded by mating or whether one mating is sufficient for an entire reproductive season. Similarly, data are absent on elapse of time between copulation and laying which might give some indication of the time of preovipositional development. However, these omissions in no way detract from an excellent study. It would be naive to expect that every phase of life history could be covered by any one study and certainly the most significant aspects are treated thoroughly.

The format and print of the book are attractive and the figures and tables, with a few exceptions, are clear and well done. The book is inexpensive and essential for every herpetologist interested in the broader aspects of his field and can be unreservedly recommended for any student of population ecology.—DONALD W. TINKLE, Department of Biology, Texas Technological College, Lubbock.

A CALIFORNIA FLORA. By Philip A. Munz in collaboration with David D. Keck. University of California Press, Berkeley and Los Angeles. 1959. 1,681 pp., frontispiece, 134 text figures. \$11.50.

This book which skillfully brings together the contributions of numerous special studies of Californian plants since the last manual of the state was published by Jepson in 1925 deserves laudatory comment. At the same time, it should be emphasized that it is not merely a compilation of the work of others but represents a careful evaluation of the various groups from extensive herbarium study and field experience. All of us who have been looking for such a volume for a number of years can be grateful to have it actually on hand.

In scope it includes all of the vascular plants known to grow spontaneously in California, and omits the nonvascular plants. More than 5500 species are described, which is an increase of about 1500 over the number listed by Jepson 35 years ago.

The most conspicuous deviations from current floras in the United States are the names given to the divisions, the delimitation of certain families, and the sequence of families, all of which reflect recent information and evaluation of the major categories and their relationships. The sequence of families may be disturbing to some who are accustomed only to the Englerian system used in most floras and herbaria in this country, but for some of the rest of us who have never taken any sequence too seriously, the present departure from tradition is refreshing and desirable, if only to indicate that no sequence should be considered sacred. For those who may have difficulty locating families with the arrangement used and find the index cumbersome for this purpose, an alphabetical list of families with appropriate page references (which can be pasted conveniently on the inside of the back cover) is available on request from the Rancho Santa Ana Botanic Garden, Claremont, California. I have found this supplementary index to be extremely convenient.

The twenty pages of introductory material are a contribution in themselves for they serve not only to orient the user of this volume but also

provide the general reader with a concise introduction to the diversity of the vegetation of California and its historical development, with the latter in the form of a very elegant and authoritative summary by Daniel I. Axelrod. The section on plant communities provides an effective and desirable basis for indicating the habitat of each species. A list of species is given for each of the plant communities but no distinction is made between species that are widespread and conspicuous elements and those that are local or relatively minor associates.

The illustrations, except for the colored frontispiece of California poppy, are limited to line drawings of good quality in a banner at the beginning of each family. The few plants illustrated have been selected to represent the most characteristic traits of the family as it occurs in California.

The descriptions in general seem to be adequate, although the treatment of polytypic species is somewhat confusing until one realizes that the description, range of distribution, and ecological association given for the "species" is in fact pertinent only to the subspecies or variety which includes the nomenclatural type of the species. Subspecies, which are of equivalent taxonomic rank, are then appended, often following a key to the subspecies (or varieties). Even then, the subspecies which includes the type is shown as being the "species," which has the effect of suggesting that the subspecies which happened to be first described is of greater importance than those subsequently discovered. Chromosome numbers are given for each taxon, and while some reports have been overlooked and no bibliography of the citations is given, the chromosome information is a welcome addition to the descriptions.

Professional botanists will have every reason to generally commend this book as a reference for their own use and for the use of other experienced botanists. On the other hand, some of us had hoped that this volume would also be a boon to instruction in identification of the native flora. Having now used it in a field botany class for a semester, I must say regretfully that it not only falls short of my hopes, but has proved discouraging to students who were initially enthusiastic at the prospect of learning to identify plants. The reasons for this are twofold. In the first place the weight of the book (about 4 lbs.) and the complexity of the keys necessary to treat such a diverse flora as that of California make it unwieldy. The necessary use of thin paper makes the pages all but unmanageable in a breeze; the large number of species and genera included requires the novice and even students of considerable experience to spend a discouraging amount of time identifying an unknown plant. For teaching purposes a regional flora of more limited scope, such as the earlier *Manual of Southern California Botany* by Munz (1935), is much to be preferred, but unfortunately this book has been out of print for a number of years.

Although the very magnitude of the *Flora* is discouraging to the student, the second basis on which they have become frustrated and have condemned it in no uncertain terms is the prevalence of innumerable typographical errors or errors in the construction of the keys which not only prevents them from identifying many plants but leaves them uncertain even when they have arrived at a reasonable answer. I do not recall a single class exercise in which some unnecessary obstacle such as omitted lines or names, interchanged lines in the keys, inconsistencies between the keys and descriptions, has not plagued the students. The professional botanist will not run into most of these frustrations for he will recognize the genus *Prunus* on sight and will not discover that it must have five carpels in order to be identified as that genus in the key to the genera of Rosaceae; he will recognize that *Erodium* belongs to the

Geraniaceae without realizing that species with pinnate leaves cannot be identified in the key to the families. On the other hand, the student rapidly loses confidence when he runs into such errors or omissions, and there is no way to reassure him. Even the professional will be disconcerted by some of the errors such as finding the same taxon described as both *Pellaea compacta* and *Pellaea mucronata* var. *californica*, with each cited as a synonym of the other.

I understand that some of the omissions, inverted type etc., are being corrected for the next binding, but what is needed is an immediate re-printing after a very careful scrutiny of the entire book with a view to correcting all errors. It is unexcusable for the University of California Press to issue a book of high scholarly merit, and an outstanding contribution to its field, which because of poor editing and proofreading has the effect of discouraging students and preventing them from gaining knowledge and intellectual satisfaction from its use.—HARLAN LEWIS, University of California, Los Angeles.

THE VEGETATION OF WISCONSIN: AN ORDINATION OF PLANT COMMUNITIES.

By John T. Curtis. xi, 657 pages and 270 maps, charts, tables and original photographs. The University of Wisconsin Press, Madison, Wisconsin. 1959. \$7.50.

When a book of over 650 pages is written about the vegetation of any region, it is a significant addition to the rather limited literature on this little-studied topic. When this book concerns itself with the vegetation of but one of the fifty United States, we might reasonably anticipate that it would probe deeply into the subject; Dr. Curtis' book is not a disappointment. Specialists who have kept abreast of developments in vegetation study in the past decade — and especially the significant published contributions of Dr. Curtis and his students and those of R. W. Whittaker — will find little that is new on the nature of vegetation. However, Dr. Curtis has woven together the descriptions and analyses of the myriad of Wisconsin's vegetation types into a very readable volume that will be highly informative to vegetation specialists as well as biologists, conservationists, agricultural specialists and intelligent laymen.

The book is divided into seven parts plus an appendix, glossary, bibliography, species list and index. The first part includes brief chapters on the flora, the environment, the plant communities and their distribution in Wisconsin and a chapter on vegetation study methods.

In the terse but well-done chapter on flora, the state is divided into a northern and a southern floristic province with a tension zone between. The following floral elements make up the state flora: Boreal, Alleghenian, Ozarkian, Prairie and Coastal Plain elements. An "epibiotic element" is made up of plants from various regions but surviving in Wisconsin on rock cliffs, lake shores, etc., and includes a Preglacial element surviving the Pleistocene in the Driftless Area. An exotic element includes primarily the weeds introduced by man.

The Preglacial element is singled out for special treatment and introduces a point on which Dr. Curtis would probably not find universal agreement among pleistocene biogeographers. On p. 14, he states, "A variety of geological, climatological and ecological evidence . . . strongly supports the hypothesis that the Driftless Area was at least partially covered with vegetation at all times and that it formed the source for the bulk of the plant cover which later spread out over the remaining parts of the state as these were deglaciated." And on

p. 11 "... that all of our major dominants survived the glacial advances in or near the non-glaciated region and subsequently spread from that center."

The vegetation treatment combines several approaches to vegetation classification. Perhaps the most characteristic aspect of the over-all treatment is that vegetation, at the outset, is approached as representing a continuous variable. Thus, the sub-divisions recognized are not discrete units but rather groupings of convenience which correspond in general with the vegetation patterns long recognized by observant field men. The community concept held is the individualistic community of Gleason and Ramensky. The primary categories are the three great physiognomic groups: forests, grasslands and savannas. In a category labeled "lesser communities" he variously uses physiognomy, physiography, species composition and land use for recognizing fen, meadow, bog, aquatic, beach, dune, cliff and weed communities. Floristic differences north and south of the tension zone lead to the northern forests, grasslands and savannas being considered as different vegetation types from their southern counterparts. The distinction takes place across the narrow tension zone which includes communities containing both floristic elements.

Dr. Curtis considers each of the major vegetation types as a continuum which was sampled extensively and without the usual bias of first deciding on the sub-units. Subsequent fractioning is accomplished from these data by recognizing more-or-less arbitrary segments along a linear arrangement of the stands. This arrangement is obtained by various computations and reflects primarily differing moisture relationships. Where the continuum is extensive and enough data available, five segments termed wet, wet-mesic, mesic, dry-mesic, and dry, respectively are discussed. By this procedure 21 major communities are recognized which together with the 13 "lesser communities" give Wisconsin a total of 34, each of which is discussed in varying detail.

The bulk of the text, part 2 through part 6, contains treatments of these 34 units. These discussions are not equally detailed since the amounts of available data are not equivalent. However, the author clearly states the degree of confidence to be assigned the various treatments.

In general the material includes a description of the composition and structure, often with excellent resumes of early accounts of the pre-settlement conditions of the type; life history sketches of some of the major species; successional relationships; associated biota; regional variations; associated environment; geographical relationships — both North America and European; origin of type; and utilization and current management of the type.

Following the individual treatments is part 7 titled, "The vegetation as a whole." It includes chapters on postglacial history, the effect of man on the vegetation and interrelations of communities. The latter chapter is of particular interest to the vegetation specialist and includes a well-written summary of the work of the author and his students on ordination of vegetation, the behavior of various non-dominant species on ordination diagrams, an inquiry into the validity of fidelity of species as a criterion for vegetation classification, and the author's conclusions concerning the nature of plant communities. These conclusions represent a vindication of the deep and precocious insight into vegetation published by H. A. Gleason and independently in Russia by Ramensky over three decades ago and essentially ignored by U.S. and European students of vegetation until recently.

One of the fine contributions of the book is the refreshing historical depth derived from a skilled use of well-chosen quotations of early observers.

Occasional wryly humorous jabs at narrowly trained technicians and bureaucratic dicta provide a light touch to serious problems. *E.g.* on p. 337, in discussing the changes taking place in the oak openings of the pre-settlement

savannas, he states, "These huge, open-grown trees tell a graphic story of an interesting phase of Wisconsin's history. It is unfortunate that many consulting foresters are so imbued with textbook silvicultural theory as to invariably recommend that forest owners remove these derisively named "wolf trees" so that more valuable (*sic*) trees may take their place. It is highly probable that an active appreciation of the history of their forests as dynamically changing biotic complexes would in the long run be of more value to the owners."

All individuals enlightened to the rapidity with which the last representative pieces of many of our natural areas are disappearing will find particularly gratifying the numerous passages following descriptions of interesting vegetation within the state, "This stand has been set aside as a Scientific Study Area by the State Board for the Preservation of Scientific Areas." Although ecologists and others have long fought to preserve blocks of natural areas as continuous reservoirs of natural experiments, this book will show a degree of organized success in Wisconsin unmatched in most states.

Geographically oriented biologists will find valuable the numerous maps showing various environmental conditions, species ranges, pre-settlement boundaries of the major vegetation types, the location of the examples studied for each type, and maps for postglacial pollen diagrams. Vegetation specialists will be gratified to find an excellent appendix which consolidates recent data from significant published and unpublished vegetation studies in the state. For most types these data include dot maps of stand locations, maps of the pre-settlement extent of the type, average composition for the type, including both tree and ground layers where present, summaries of two typical stands for the type, and a resume including important vegetation, geographic, environmental and bibliographic statistics for the type.

The book is singularly free of the typographical and other errors that first printings usually have. One that is obvious occurs on p. 99, Fig. 10, where the ordination on the abscissa would appear to be from wet on the left through mesic in the center to dry on the right. However, the right hand end is labeled "M" as is the middle. Another, more bothersome point is the series of disagreements between the stated numbers of stands representing the study material. *E.g.*, Figure VIII-1 shows approximately 108 dots for Southern Lowland Forest while table IV-2 shows 16 stands of Southern Forest-Wet and 64 stands of Southern Forest-Wet Mesic; on p. 133 the text mentions 127 Xeric forest stands, the dot map (Fig. VII-1) on p. 522 shows 110 dots and table IV-2 on p. 517 shows 30 stands for Southern Forest-Dry and 54 stands for Southern Forest-Dry mesic. Similar disagreements occur for Southern Mesic Forest, Northern Lowland Forest, Northern Mesic Forest, Northern Boreal Forest and Mesic Prairie. There is probably a good explanation for these differences but a note in the appendix would allay the readers' suspicion that an error in computation is the cause.

The type is large, the paper and binding of good quality, and the illustrations, well chosen. The vegetation photographs in particular form an attractive and useful part of the book. The glossary includes most terms likely to be unknown to the average educated reader. The bibliography covers 25 pages and includes publications of Australian, Canadian, British, German, Swedish, Polish, Russian, Dutch, French, Austrian, Japanese, Swiss, Danish, Norwegian and Finnish nationality, as well as a wide array of United States entries. An alphabetically arranged species list is included which designated the number of communities in which the species occurs and a symbol indicates the native community in which it achieves its maximum presence. The index is unusually complete, including page references for major species, vegetation types, authors, geographic names and the biological terms used.

In summary, this book is, in the reviewer's opinion, the best treatment of the vegetation of any of the 50 United States and will serve as a useful reference and guide for students of vegetation, biologists and others for many years. Its weaknesses stem primarily from the condition of man's current knowledge of the vegetation rather than from inadequacies of the author.—JOHN E. CANTLON, Michigan State University, East Lansing.

THE ANTECEDENTS OF MAN: An Introduction to the Evolution of the Primates.  
By W. E. Le Gros Clark. Quadrangle Books, Chicago. 374 pp., 152 figs.  
1960. \$6.00.

Contained in the pages of this book is the substance of the Munro Lectures presented at the University of Edinburgh in 1953. More recent findings have been added. Basically the book is similar to the author's *The Early Forerunners of Man* (1934). After informative opening chapters on the evolutionary process and brief biographies of fossil and contemporary primates with the erection of a primate family tree, there follow chapters on the comparative morphology of the dentition, skull, limbs, brain, special senses, digestive system, and reproductive system. The terminating chapter is a discussion of evolutionary radiations of the group.

The tree-shrews receive considerable attention. All the evidence for including them in the primates is carefully presented, and it seems conclusive. Modern primates receive more attention than do the relatively rare extinct forms. The comparative anatomy of modern forms has yielded indirect evidence of the evolutionary history of the group. Paleontological evidence seems also to indicate that the primate sequence was: tree-shrew-like ancestors—to lemur-like—to tarsier-like—to cercopithecoid-like—to pongid-like and culminating (in the Pleistocene) in the hominids.

The book, according to the author, is "an introductory textbook which is intended for students of whom some may have no special knowledge of comparative anatomy." Because the author has made an effort carefully to explain and/or illustrate the anatomical structures which he discusses, the book could be used successfully as a "text" in an introductory Physical Anthropology course. To apply the term "textbook" to a publication, however, is usually to stigmatize it as far as the general reader is concerned. This I do not wish to do. I feel the general reader interested in his biological background will find the contents interesting and the author most articulate.—GEORGE R. BERNARD, Department of Gross Anatomy, Medical College of Georgia, Augusta, Georgia.

NOMENCLATURE OF PLANTS. By Harold St. John. Ronald Press, N.Y. 1958.  
157 pp. \$2.50.

When Henry Van Dyke wrote that "naming things is one of the oldest and simplest of human pastimes" he did not contemplate the International Code of Botanical Nomenclature. Professor St. John's little book is a kind of game book, designed for advanced botany classes where what he views as the fun of nomenclature is played. Honestly there are not likely to be many such games played around the world, if, indeed, there exist many advanced classes in plant taxonomy where the boards might be set up. When the cards are down most instructors in plant taxonomy would rather devote the precious few hours of their class to the handling of living plant materials, cherishing every moment for direct contact with the angiosperm creation in

all its varied forms. But there are always a few minds, as every teacher has discovered, who are fascinated by the application of essentially legal decisions to the names of organisms. The challenge is there but also the risk of excesses. It is unfortunate only when attention to nomenclature pushes aside the more important consideration of plant morphology, patterns of evolution, and the like.

The subtitle, "A Text for the application by the case method of the International Code of Botanical Nomenclature," sets the book's target. Chapter One explains the working of the Code and how it may be applied to a sample nomenclature case. Chapter Two contains all the principles encountered in the 1956 Code and, if there is time for one set of cases in the course of study, this chapter should be selected to demonstrate the rules in action. Chapter Three concerns the application of the rules to cryptogams; the remaining four chapters are lists of miscellaneous cases additional to those presented in the second chapter. Errors in typography are fortunately few, especially in view of the nature of the references. The interesting case of *Prosopis pubescens* Benth. in Hook., London Jour. Bot. 5:82. 1846 versus *Prosopis odorata* Torr. & Frem. in Fremont, Second Report 313 pl. 1. 1845, is an addendum that some instructors may find worth noting down on the blank pages provided at the back of this boundless subject. There was a decade in American botany when *nomen calare*, name calling, or the proper basis of nomenclature, moved over from the plant to the plantsman. Each succeeding International Botanical Congress moves a little closer to the Utopia when names, applied under a minimum of rules with a modicum of exceptions—officially "Nomina conservanda"—will serve their true function: linguistic handles of the utmost possible stability, applied in an imperfect world, for the communication among men of serious intentions concerned with the accurate recognition of organisms.—JOSEPH EWAN, Tulane University, New Orleans.

## Books Received

- CAVES OF ADVENTURE. Haroun Tazieff. Viking Press, Inc. 222 p., 16 illus. 1960. \$1.45, U. S. \$1.69, Canada.
- ADVENTURING WITH BEEBE. William Beebe. Viking Press, Inc. 282 p., 15 illus. 1960. \$1.25, U. S. \$1.45, Canada.
- MANUAL FOR OUTDOOR LABORATORIES: The Development and Use of School-grounds as Outdoor Laboratories for Teaching Science and Conservation. Richard L. Weaver, Ed. Interstate Printers & Publishers, Inc. 81 p. 1959. \$1.25.
- LEAD POISONING AS A MORTALITY FACTOR IN WATERFOWL POPULATIONS. Frank C. Bellrose. Illinois Natural History Survey Bulletin. State of Illinois. 286 p. 1959.
- RAINBOW TROUT IN MEXICO AND CALIFORNIA WITH NOTES ON THE CUT-THROAT SERIES. Paul R. Needham and Richard Gard. University of California Press. 108 p., 40 figs. and 8 plates. 1959. \$2.50.
- AN ECOLOGICAL ANALYSIS OF THE AVIFAUNA OF ST. LAWRENCE ISLAND ALASKA. Francis H. Fay and Tom J. Cade. University of California Press. 77 p., 3 figs. and 5 plates. 1959. \$1.50.
- TERTIARY STRATIGRAPHY OF THE BLAIRSDEN QUADRANGLE PLUMAS COUNTY, CALIFORNIA. Cordell Durrell. University of California Press. 31 p., 1 fig. 5 plates and 5 maps. 1959. \$1.00.
- THE LOVEJOY FORMATION OF NORTHERN CALIFORNIA. Cordell Durrell. Uni-

- versity of California Press. 27 p., 1 plate and 4 maps. 1959. \$1.00.
- PLIOCENE AND LOWER PLEISTOCENE OF THE WESTERN PART OF THE SAN FRANCISCO PENINSULA. William Glen. University of California Press. 51 p., 5 figs., 2 plates. 1959. \$1.00.
- MANUAL OF COMPARATIVE ANATOMY. Bruce M. Harrison. C. V. Mosby Co. 352 p., and 122 drawings. 1959. \$3.95.
- MEET THE SOUTHWEST DESERTS. Philip Welles. Dale S. King, Publisher. Globe, Arizona. 82 p., numerous photographs. 1960. Paper, \$1.00. Cloth, \$2.25.
- REPTILES: LIFE HISTORY, EVOLUTION AND STRUCTURE. Angus d'A. Bellairs. Harper Torchbook: The Science Library. Harper and Brothers, New York. 184 p. 1960. Paper, \$1.35.
- ANIMALS SPECIES AND THEIR EVOLUTION. A. J. Cain. Harper Torchbook: The Science Library. Harper and Brothers, New York. 183 p. 1960. Paper, \$1.35.
- PROBLEMS OF LIFE: AN EVALUATION OF MODERN BIOLOGICAL AND SCIENTIFIC THOUGHT. Ludwig von Bertalanffy. Harper Torchbook: The Science Library. Harper and Brothers, New York. 204 p. Paper, \$1.35.
- ANIMAL GROWTH AND DEVELOPMENT. Maurice Sussman. Foundations of Modern Biology series. Prentice-Hall, Inc., New York. 105 p. Illus. 1960. Paper, \$1.50.
- THE CELL. Carl P. Swanson. Foundations of Modern Biology Series. Prentice-Hall, Inc., New York. 103 p. Illus. 1960. Paper, \$1.50.
- AN ANALYSIS OF INTRASPECIFIC VARIATION IN THE KANGAROO RAT *DIPODOMYS MERRIAMI*. William Z. Lidicker, Jr. University of California Press, Berkeley and Los Angeles. Vol. 67(2), p. 125-218, plates 9-12, 20 figs. 1960. Paper, \$2.00.
- ECOLOGY OF THE PEREGRINE AND GYRFALCON POPULATIONS IN ALASKA. Tom J. Cade. University of California Press, Berkeley and Los Angeles. Vol. 63(3), p. 151-290, plates 17-26, 7 figs. 1960. Paper, \$2.50.
- HAWKS AND OWLS: POPULATION TRENDS FROM ILLINOIS CHRISTMAS COUNTS. Richard R. Graber and Jack S. Golden. Natural History Survey Division. Urbana, Illinois. 24 p. 1960.
- WINTER FOODS OF THE BOBWHITE IN SOUTHERN ILLINOIS. Edward J. Larimer. Natural History Survey Division, Urbana, Illinois. 35 p. Illus. 1960.
- A FIELD LIST OF BIRDS OF THE DETROIT-WINDSOR REGION. By Ralph A. O'Reilly, Jr., Neil T. Kelley and Alice H. Kelley. Cranbrook Institute of Science, Bloomfield Hills, Michigan. 40 p., 1 map. 1960. \$0.50.

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